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Host Preferences of *Drino bohemica* Mesn. (Diptera: Tachinidae), with Particular Reference to Olfactory Responses¹

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Many factors influence the host preferences of entomophagous insects and have an important role in determining the fate of parasites in the field. Some of the factors influence the ability of parasites to locate their hosts. Others determine the suitability of the host as a medium for larval development (7, 15, 18, 26, 27, 31). These factors together determine the range of hosts attacked and control the degree to which nonpreferred hosts are selected.

A number of factors influence the degree of preference for certain hosts. Some cause parasites to select one host species rather than a second when both occur simultaneously in the same environment (6, 16, 25). Others cause parasites to choose a particular macro-environment in which only certain hosts occur; parasites may be attracted first by the food of the host rather than the host (4, 11, 14, 16). The degree to which entomophagous insects attack different hosts may therefore be influenced by the relative attractiveness of the food on which their hosts are feeding.

Olfactory conditioning may have an influence on the choice of hosts. The term *conditioning* in relation to the selection of hosts by insects is generally used for the effect that association with a host has had on the sensory system of an insect whose choice of host has been influenced by such association. The association may occur during preimaginal development or during the emergence of adults (25). The effect is primarily through the olfactory senses (20, 21, 25). Walsh (29), who proposed the host selection principle, considered the adult female to be attracted for oviposition to the particular species on which she fed as a larva. In this paper *conditioning* concerns an effect on the parasite that results in a change in preference for a particular species of host.

Conditioning has been reported in both phytophagous and entomophagous insects but it does not occur in all species. In phytophagous species, conditioning has been reported by Craighead (1), Hopkins (9), and Thompson and Parker (18); Crombie (2) and Larson (12) were unable to induce conditioning in the species they studied. Similarly with entomophagous species, Thorpe and Jones (25) obtained conditioning in *Idechthis canescens* (Grav.) but Salt (16) was unable to induce conditioning in *Trichogramma evanescens* Westw. Findlayson (6) was able to condition the parasite *Cephalonomia waterstoni* Gahan to one but not to a second species of *Laemophloeus* beetle.

The degree of conditioning obtained by different authors also varied considerably. In phytophagous species, Hopkins (9) and Craighead (1) reported high degrees of conditioning with cumulative increases in preferences for new hosts. Thompson and Parker (18) found a small degree of conditioning in *Pyrausta nubilalis* (Hbn.) without any change of preferred host. No case of cumulative conditioning has been reported for entomophagous species, but slight degrees of conditioning among some parasites have been recorded (6, 25).

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The duration of conditioning has also varied considerably in different species. Natural loss of conditioning in *I. canescens* required ten days (21). Conditioning in the blowflies *Calliphora erythrocephala* (Mg.) and *Lucilia sericata* (Mg.) was lost during the preoviposition period (3). Dethier and Chadwick (5) observed that several workers had conditioned insects by associating a stimulus with the presence of food but emphasized that these associations seldom persisted more than a few hours. These examples show conditioning of some species to be of relatively short duration in contrast with the persistent and cumulative conditioning reported by Craighead (1) and Hopkins (9).

This is a report on a study of the host preferences of a dipterous parasite, *Drino bohémica* Mesn., and of factors that influence its preferences. Like many entomophagous insects, *D. bohémica* will attack several species of hosts. It prefers certain hosts although it can complete development on some other species. These characteristics make it a particularly suitable species with which to study the factors that influence the choice of hosts by entomophagous insects and the controversial subject of preimaginal conditioning.

Materials and Methods

The parasites used were taken from a line founded from the progeny of one mated female propagated in the laboratory for twenty generations before commencement of the study. A group that had been propagated on *Neodiprion sertifer* (Geoff.) for the three generations that preceded the study was used as the parental stock. Four lines of parasites were developed from the parental stock by propagating each line on a different species of sawfly. The sawfly species and the preferred food tree of each were: *Diprion hercyniae* (Htg.), white spruce, *Picea glauca* (Moench) Voss; *Neodiprion lecontei* (Fitch), red pine, *Pinus resinosa* Ait.; *N. sertifer*, Scots pine, *Pinus sylvestris* L.; and *Neodiprion swainei* Midd., jack pine, *Pinus banksiana* Lamb. A fifth species, *Pristiphora geniculata* (Htg.), the mountain ash sawfly was used during tests with parasites of the parental stock but no line of parasite was developed on this host.

A second group of parasites was used to obtain values for a stock not conditioned to any of the hosts used in this study; they had been propagated on the five species of sawflies some on one host and the remainder on other hosts. Parasites that emerged from the five species were mixed, permitted to mate and then propagated as in the previous generation. The third generation of these parasites was used as a check to show the preferences of a parental stock for *N. sertifer*.

Sawfly larvae were collected in the field and placed in cold storage as soon as their cocoons had been spun. These larvae were moderately active and positively phototactic when removed from their cocoons. The parasites readily attacked them. Although all larvae were handled similarly, those used in experiments were carefully selected to ensure that the degree of attractiveness of each species was not due to differences in the physical or physiological state of the larvae. Larvae that already showed evidence of parasitism were discarded.

Three series of experiments were conducted, each designed to test in a different way the preferences of *D. bohémica* for the different species of sawflies. Tests were conducted with parasites from the parental stock, from four successive generations of the lines reared on *D. hercyniae* and *N. sertifer*, and from three generations reared on *N. swainei*. The line developed on *N. lecontei* was bred continuously on this host for 28 generations but tests were not made with all of them because of seasonal interruptions. The occurrence and duration of conditioning were determined by differences in the degree of

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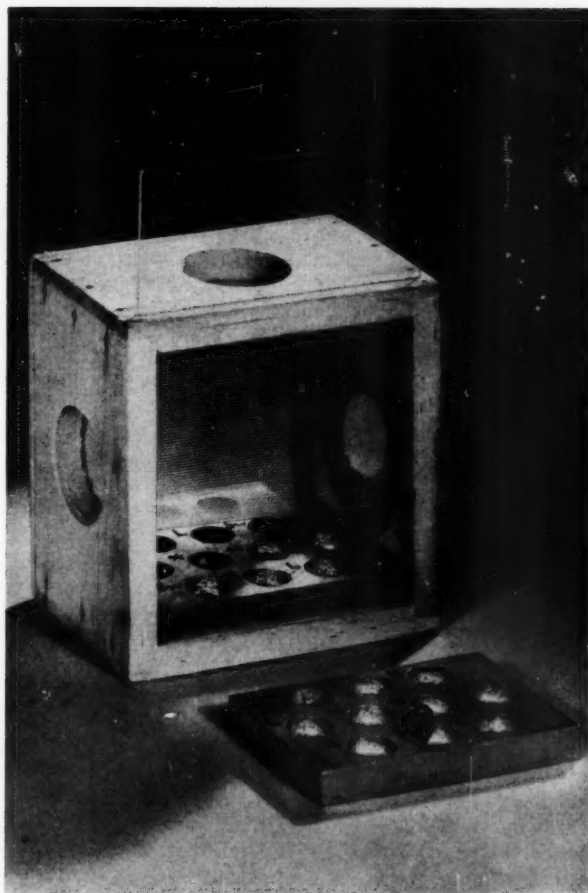


Fig. 1. Cage and blocks used in random assortment tests.

preference of parasites from successive generations for the host on which they developed. The results were analyzed by chi-square tests using the Brant-Snedecor method. All newly emerged adults were protected from exposure to test odours during their preoviposition period to prevent them from becoming conditioned or deconditioned as occurred in *I. canescens* (20).

Of the three definite categories of chemoreceptors, olfactory, gustatory, and chemical (5), only the olfactory stimuli were tested separately. For the purpose of this paper, gustatory, chemical and tactile stimuli are referred to as *chemotactile stimuli*.

Tests with Random Assortments of Larvae

Tests of host preferences when both chemotactile and olfactory stimuli were involved were conducted in small cages (Fig. 1) in which random assortments of larvae were exposed to attack by the parasites. Larvae were placed on thin blocks of wood, in ten lettered holes about one-eighth of an

inch deep. Two larvae of each species were placed on each block. The cages were arranged into series of four, each cage in a series having a different arrangement of larvae.

Three gravid females were placed in each cage and tested for one hour, twice daily, during four weeks commencing at the end of the preoviposition period. Fresh larvae were used for each test.

Preferences of the females were determined by counting the number of eggs deposited on each species. As this parasite deposits only one egg during an attack, the eggs laid indicated the number of times each host was selected. Tests had shown that oviposition by one female did not increase or decrease the attractiveness of the attacked larva for other females. The degree of response to each host species was calculated as a percentage of the total number of eggs deposited on all hosts.

Tests in the Olfactometer

Tests of host preferences when only olfactory stimuli were involved were conducted in a Y-tube type (13) of olfactometer. The apparatus (Fig. 2) was a modification of that used by Thorpe and Jones (25) and Thorpe (20). One modification was the use of a pressure system rather than a vacuum system as used by Thorpe. Thorpe (20) objected to a pressure system because it required the use of rubber tubing, which might mask odours of the host. This disadvantage was eliminated by the use of nonreactive Tygon (U.S. Stoneware Company, Akron, Ohio) tubing, which is odourless. Another modification was that air from the pump passed through the entire length of the olfactometer whereas in the apparatus used by Thorpe and Jones (25) it was drawn off through the side at the base of the Y-tube. Hence, the air flowed past the test insects before they entered the base of the Y-tube and exposed them to test odours for a longer period before they could enter either arm of the Y-tube.

The air was filtered and passed through distilled water before entering the olfactometer. It then flowed through Dreshel gas-washing bottles (Central Scientific Company, Toronto, Ontario) (Fig. 2, A), which held the sources of test odours. The flow of air was controlled by flow-meters (B) as in the equipment used by Weiting and Hoskins (30). Total flow of air was 900 cc. per minute. The two air currents converged in the Y-tube (C), passed through the main cylinder (D) and through the screened piston (F), and escaped through the screen cap (E). The third air line (G) did not have a flow-meter as in the olfactometer used by Weiting and Hoskins, since it was used only to increase the flow of clean air to both arms of the Y-tube while the equipment was being flushed between tests.

Flies could be gradually confined to the funnel area by means of the piston (F) so that they would more likely find their way into the base of the Y-tube if attracted by test odours. The diameter of the Y-tube was large enough to permit flies to pass without disturbing one another, but small enough to discourage flying. If the parasites had been permitted to fly they might have entered an arm of the Y-tube without making a definite choice. In each test some of the parasites did not respond.

Tests were conducted in the following manner. Parasites were introduced into the main cylinder and left for a short period to recover from any effects of handling. Each test, initiated by starting the air flow and then turning on the light in the olfactometer, lasted 20 minutes. After every test the flies were blown back into the main cylinder, where they were able to rest while the olfactometer was flushed with clean air. The cleaning process was continued

for 15 minutes between tests. Each test was followed by a second test with the same flies, the side through which the odours were carried being reversed. To avoid the effect of fatigue, no group of parasites was used for more than one pair of reciprocal tests during any half-day period.

Preferences of the parental stock for the odour of each species of host were tested in the olfactometer in three ways: against the odour of a standard

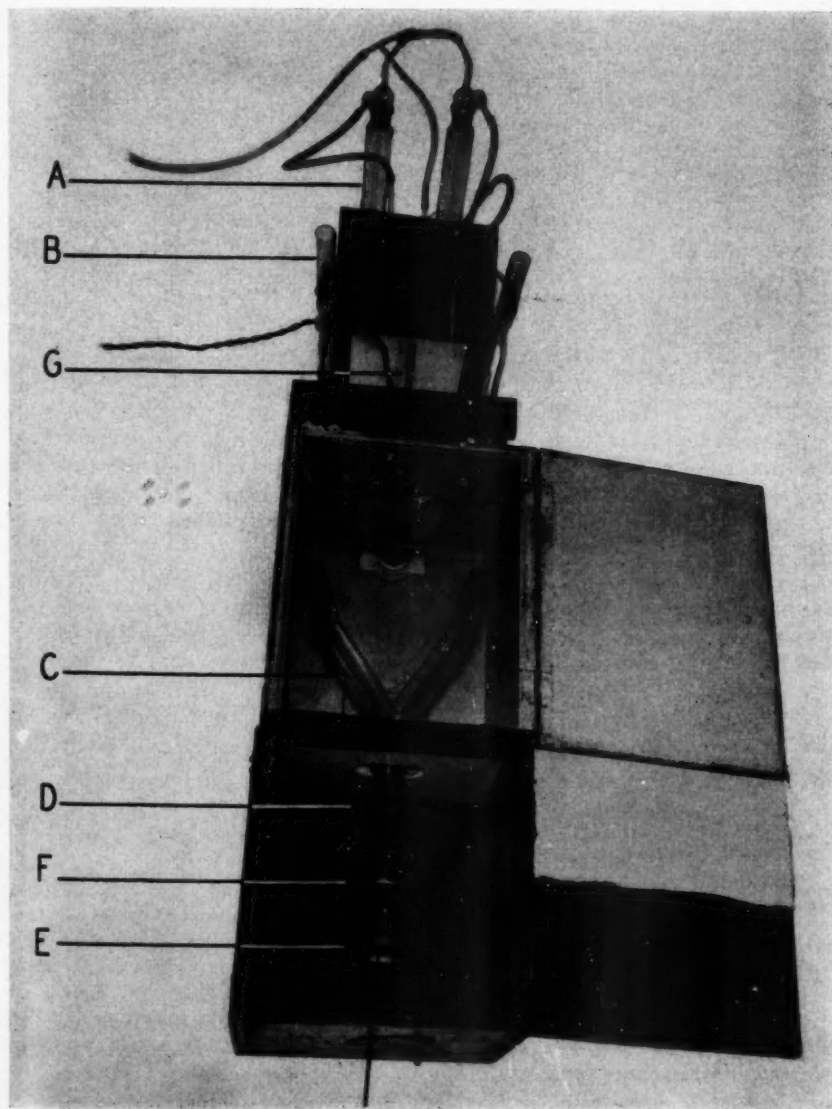


Fig. 2. The olfactometer with A, gas-washing bottles; B, flow-meters; C, Y-tube; D, main cylinder; E, screened cap; F, screened piston; G, central airline.

solution of pine needle oil, against a current of odourless air (8), and against each other in pairs of species. The standard solution of pine needle oil was prepared by diluting the concentrate with nugel oil so that the odour of 5 cc. was less attractive than that of the most frequently selected host species but more attractive than that of the nonpreferred hosts.

Preferences of subsequent generations of the four lines for the odour of the host on which the parasites developed were determined by testing the species in pairs.

Tests with Food Trees of Hosts

The influence of the food plants of the hosts on the preferences of *D. bohémica* was tested in two ways. First, the olfactory attractiveness of the food plants to the parasite was determined by testing the odour of each plant against the odour of the standard pine needle oil solution. Austrian pine, *Pinus austriaca* A. & Gr., was included to determine what the reaction of the parasites would be to a tree on which its hosts do not feed. The second way was to measure the percentage parasitism of each host while on its preferred food tree. Small trees were enclosed in a cage 6 ft. square and 3½ ft. high (Fig. 3). The floor of the cage was made of medium-weight duck. The fabric was fitted around the trunks of the trees with zippers so that the boxes of soil in which the trees were growing were beneath the cage. All trees had approximately equal areas of needle surfaces. Although light intensity was approximately equal on all sides, the positions of the trees in the cages were changed to avoid possible position effects.

Twelve larvae of each host species were placed on their preferred food tree for each test. They were distributed uniformly throughout the trees and held in a fixed position on the needles by a fine thread looped around the middle of the body. This was necessary to prevent larvae from falling to the floor of the cage, where they would be repeatedly attacked.

Twelve parasites were put into the cage for each test and left there for 24 hr. Preferences were calculated from the number of attacks on each species. Eggs of *D. bohémica* were easily detected even though the parasite had hatched and entered the host, the chorion remaining attached to the body.

The F2 to F4 generations of the line reared on *D. bercyniae* and the F3 to F19 generations reared on *N. lecontei* were tested to determine whether continuous breeding on one host species would change the degree of preference shown by *D. bohémica* for the food tree of that host.

Preferences of the Parental Stock

Random Assortments of Larvae

Responses of the parental stock propagated on *N. sertifer* to the three species of sawfly larvae exposed to them were:—

Sawfly	<i>N. lecontei</i>	<i>N. sertifer</i>	<i>D. bercyniae</i>
Number of attacks	301	287	136
Percentage of attacks	41.6	39.6	18.8

The chi-square test showed that the differences in the selection of hosts were highly significant ($P < .005$), the order of preference being *N. lecontei*, *N. sertifer* and *D. bercyniae*.

The stock propagated on five hosts showed degrees of preference for the four species of larvae exposed to them. The selection of hosts when the parasites were not conditioned to one of these species was:—

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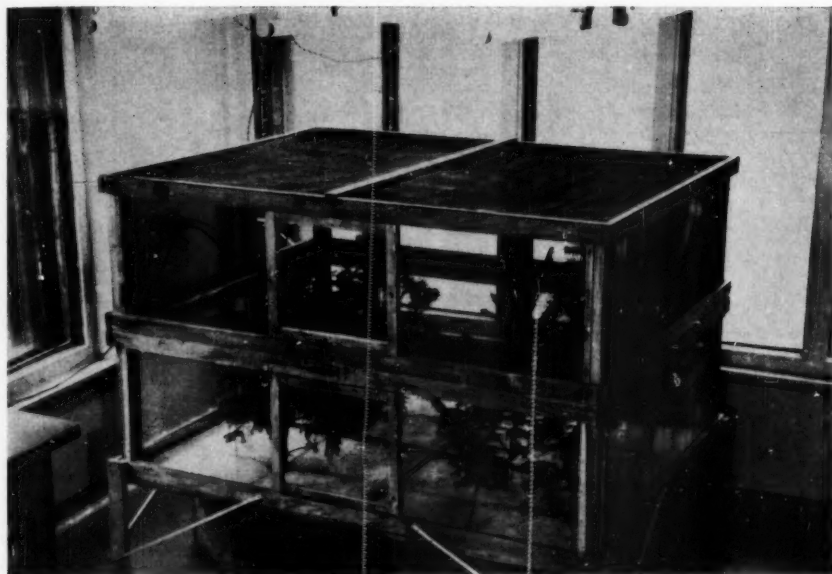


Fig. 3. Cage with trees in position for testing the influence of food plants of the hosts on host selection.

Sawfly	<i>N. lecontei</i>	<i>D. hercyniae</i>	<i>N. swaini</i>	<i>N. sertifer</i>
Number of attacks	577	378	362	262
Percentage of attacks	36.9	23.6	22.7	16.7

Differences in the selection of hosts were highly significant ($P < .005$), the order of preference being *N. lecontei*, *D. hercyniae*, *N. swaini* and *N. sertifer*. The order for *N. lecontei* and *D. hercyniae* was the same in both groups.

Olfactometer Tests

Tests with the standard pine needle oil and with odourless air did not measure the differences in the olfactory attractiveness of the various host larvae. When the pine needle oil was used, the chi-square test indicated no significant difference ($P > .08$) in the percentage response to the various species (Table I). Since the flies entered the arms of the Y-tube in approximately equal numbers, that is 50% to each arm, when there was no attractive or repellent odour in either arm, the degree of preference for one odour over another was, therefore, indicated by the difference in the number or percentage of flies that entered each arm. In tests with the pine needle oil, responses to the odour of host larvae were less than 50% for each of the hosts. It seems, therefore, that the attractiveness of the pine needle oil reduced differences in the attractiveness of the different larvae below the level of significance.

In tests with odourless air as the standard the odour of each species was attractive to the parasites but the odourless air was not. The percentage response to each species was well over 50 (Table I) and the differences were not significant ($P > .57$).

The parental stock exhibited definite degrees of preference for five species of sawfly larvae during paired-species tests. Each percentage response above

TABLE I

Percentage responses of parental stock of *D. bohémica* to odours of sawfly larvae in preference to standards

Standard	Species	Number of flies responded	Responses to odour of larvae, %
Pine needle oil	<i>N. lecontei</i>	56	42.9*
	<i>D. hercyniae</i>	52	46.2
	<i>N. sertifer</i>	44	22.7
	<i>N. swainei</i>	60	43.3
Odourless air	<i>N. lecontei</i>	56	71.4**
	<i>D. hercyniae</i>	84	80.9
	<i>N. sertifer</i>	52	76.9
	<i>N. swainei</i>	72	77.8

* χ^2 (between species) = 6.77; $P > .08$.

** χ^2 (between species) = 1.78; $P > .57$.

50 was considered as a positive value, below 50 as negative. These values were totalled for each species (Table II). This method of calculating attraction is similar to that used by McIndoo (13), Hoskins and Craig (10) and Willis (32). These authors interpreted a response of less than 50% as repellency. In the current study none of the hosts were repellent, the values below 50 are designated as negative to facilitate the comparison of degrees of preference.

The differences in the degrees of preference for these hosts (Table II) were clearly evident when calculated in this manner. The order of preference was *D. hercyniae*, *N. lecontei*, *N. swainei* and *N. sertifer*. The degree of preference for *D. hercyniae* was much higher than the value for the other species.

The percentage response to *P. geniculata* was low in all cases, the total degree of response being -37.0. The low response to the odour of this species is in agreement with the low percentage of selection of this host during tests with random assortments of larvae (unpublished data).

Preferences of Filial Generations

Random Assortment Tests

There were significant differences in the responses to *N. lecontei* ($P < .005$) by parasites from successive generations reared on this host (Table III). *F1* parasites had an increased preference for *N. lecontei*, an indication of conditioning toward this host. The preference of *F2* parasites was lower than that of parasites of the *F1* but not significantly higher than the parental stock. The degree of preference by parasites of the *F2*, *F3*, and *F4* remained constant, varying by less than 1%. The degrees of preference for *N. lecontei* by parasites of the *F5* and *F8* generations were at a level significantly lower than that of the parental stock. Preferences of parasites from later generations fluctuated (Table III) but remained below the level of the parental stock and became progressively lower to and including the twenty-sixth generation. Evidence of conditioning to *N. lecontei* was apparent only during the *F1* generation.

TABLE II

Degrees of preference of parental stock of *D. bohémica* to odours of sawfly larvae during paired-species tests

Responses to <i>D. hercyniae</i>			Responses to <i>N. sertifer</i>		
Test	%	Degree	Test	%	Degree
<i>D. hercyniae</i>			<i>N. sertifer</i>		
vs. <i>N. lecontei</i>	56.8	+ 6.8	vs. <i>N. lecontei</i>	37.3	-12.7
<i>N. sertifer</i>	72.3	+22.3	<i>D. hercyniae</i>	40.7	- 9.3
<i>N. swainei</i>	69.2	+19.2	<i>N. swainei</i>	41.2	- 8.8
<i>P. geniculata</i>	55.6	+ 5.6	<i>P. geniculata</i>	65.6	+15.6
		$\Sigma +53.9$			$\Sigma -15.2$
Responses to <i>N. lecontei</i>			Responses to <i>N. swainei</i>		
<i>N. lecontei</i>			<i>N. swainei</i>		
vs. <i>D. hercyniae</i>	43.2	- 6.8	vs. <i>N. lecontei</i>	58.3	+ 8.3
<i>N. sertifer</i>	64.7	+14.7	<i>D. hercyniae</i>	30.8	-19.2
<i>N. swainei</i>	41.7	- 8.3	<i>N. sertifer</i>	53.1	+ 3.1
<i>P. geniculata</i>	58.6	+ 8.6	<i>P. geniculata</i>	57.2	+ 7.2
		$\Sigma + 8.2$			$\Sigma - 0.6$
Responses to <i>P. geniculata</i> $\Sigma -37.0$					

TABLE III

Percentages of eggs deposited on four species of hosts during random assortment tests with *D. bohémica* from successive generations reared on *N. lecontei*

Generation	Number of eggs deposited	Eggs deposited, %			
		<i>N. lecontei</i>	<i>N. sertifer</i>	<i>D. hercyniae</i>	<i>N. swainei</i>
<i>P</i>	724	41.6*	39.6	18.8	—
<i>F1</i>	892	47.1	26.9	8.6	17.5
<i>F2</i>	666	43.2	19.2	20.0	15.6
<i>F3</i>	849	43.5	16.2	18.6	21.7
<i>F4</i>	512	43.7	13.9	24.4	18.0
<i>F5</i>	355	38.6	14.6	32.7	14.1
<i>F8</i>	377	29.2	14.3	36.1	20.4
<i>F9</i>	662	37.9	15.3	30.8	16.0
<i>F15</i>	909	29.5	13.1	39.3	18.2
<i>F16</i>	901	39.2	14.3	30.6	15.9
<i>F17</i>	410	29.3	14.1	40.0	16.5
<i>F18</i>	1,530	25.9	14.2	46.4	13.3
<i>F19</i>	1,459	24.7	12.3	47.1	15.8
<i>F26</i>	149	21.5	12.1	46.3	20.1
<i>F27</i>	532	40.4	8.1	33.8	18.4
<i>F28</i>	265	38.5	13.6	37.3	10.6

* χ^2 (between generations) = 310.14; $P < .005$.

There was a marked increase in the degree of preference for *N. lecontei* by parasites of the *F27* and *F28* generations with no significant difference between the preferences of parasites of these two generations and the parental stock. Changes in the responses to *N. lecontei* were in the nature of a cycle, with conditioning in the *F1*, followed by a fluctuating but decreasing preference to the *F26*, then a return to the level of the parental stock in the *F27* and *F28*.

The degrees of preference for *D. hercyniae* by parasites reared on this host, *F1*–*F4* inclusive, were significantly higher than that of the parental stock ($P < .005$) (Table IV). The degree of preference for *D. hercyniae* by parasites of the *F3* was higher than that of the *F2* but the *F4* was lower than the *F3*; the *F4* was still higher, however, than that of the *F2*. Conditioning was apparent in the *F2*, *F3*, and *F4* but less pronounced in the *F4*.

TABLE IV

Percentages of eggs deposited on four species of hosts during random assortment tests with *D. bohemia* from successive generations reared on *D. hercyniae*

Generation	Number of eggs deposited	Eggs deposited, %			
		<i>D. hercyniae</i>	<i>N. sertifer</i>	<i>N. lecontei</i>	<i>N. swainei</i>
<i>P</i>	724	18.8*	39.6	41.7	—
<i>F1</i>	532	26.9	17.1	42.8	13.1
<i>F2</i>	815	28.3	16.2	33.4	22.1
<i>F3</i>	400	37.2	16.2	22.7	23.7
<i>F4</i>	372	34.1	15.3	33.0	17.5

* χ^2 (between generations) = 54.79; $P < .005$.

There were increases in the degree of preference for *N. swainei* by parasites from successive generations developed on this host (Table V) but the differences were too small to be significant ($P > .39$). Although the differences between the preferences by successive generations were not significant the changes appeared to parallel those found in the lines reared on *N. lecontei* (Table III) and on *D. hercyniae* (Table IV).

TABLE V

Percentages of eggs deposited on four species of hosts during random assortment tests with *D. bohemia* from successive generations reared on *N. swainei*

Generation	Number of eggs deposited	Eggs deposited, %			
		<i>N. swainei</i>	<i>D. hercyniae</i>	<i>N. lecontei</i>	<i>N. sertifer</i>
<i>P</i>	252	22.2*	21.8	34.1	21.8
<i>F1</i>	367	28.3	24.5	36.0	11.2
<i>F2</i>	130	26.9	22.3	34.6	16.1
<i>F3</i>	330	25.1	21.5	35.4	17.9

* χ^2 (between generations) = 3.14; $P > .39$.

The degree of preference for *N. sertifer* by parasites of the *F3* to *F7* generations reared on this host were significantly higher than that of the parental stock ($P < .005$). Parasites of the *F3* generation had the highest degree of preference for *N. sertifer*. Preferences by the *F6* and *F7* generations were higher than that of the *F4* and *F5* but were about 13% less than that of the *F3* generation. The influence of conditioning was apparent in all generations but decreased after the *F3*. The increased preference for this host followed by decreased and fluctuating degrees of preference was similar to the conditioning obtained with parasites from the line reared on *N. lecontei* (Table VI).

TABLE VI

Percentages of eggs deposited on four species of hosts during random assortment tests with *D. bohemicus* from successive generations reared on *N. sertifer*

Generation	Number of eggs deposited	Eggs deposited, %			
		<i>N. sertifer</i>	<i>D. hercyniae</i>	<i>N. lecontei</i>	<i>N. swaini</i>
<i>P</i>	1,579	16.7*	23.6	36.9	22.7
<i>F3</i>	724	37.6	18.8	41.6	—
<i>F4</i>	252	21.8	21.8	34.1	22.2
<i>F5</i>	179	19.5	20.1	46.9	13.4
<i>F6</i>	577	24.6	19.8	28.4	27.2
<i>F7</i>	377	23.6	23.3	33.7	19.4

* x^2 (between generations) = 71.64; $P < .005$.

Paired-Species Tests

The degrees of preference for the odour of *N. lecontei* by parasites reared on this host, as determined by paired-species tests, were different in successive generations (Table VII). The number of attacks on *N. lecontei* by parasites of each generation when tested against each of the four other species have been totalled and a mean response for each generation calculated.

There was a slight increase in the preference for this host by parasites of the *F1* generation but it was not significant ($P > .32$). There was a significant increase in the preference for *N. lecontei* between the parental and the *F2* generations ($P < .02$). There were no significant differences between the preferences of the *F3*, *F8* or *F9* generations and the parental stock ($P > .16$, .32 and .16 respectively). A significant increase in the degree of preference for *N. lecontei* was evident only in the *F2* generation.

The degrees of preference for the odour of *D. hercyniae* by successive generations of parasites bred on this host were different (Table VIII). There was a significant increase in the preference of parasites from the *F1* generation over that of the parental stock ($P < .01$). The preferences of the *F2* and *F3* generations were not significantly different from that of the parental stock ($P > .32$ in each case). An increased preference for *D. hercyniae* was evident only in the *F1* generation.

TABLE VII

Percentage responses to *N. lecontei* during paired-species tests with *D. bohémica* from successive generations reared on *N. lecontei*

Test	Responses to <i>N. lecontei</i> , %						
	Parent		<i>F1</i>	<i>F2</i>	<i>F3</i>	<i>F8</i>	<i>F9</i>
<i>N. lecontei</i> vs. <i>D. hercyniae</i>	43.2		33.3	45.4	44.7	58.8	57.9
<i>N. lecontei</i> vs. <i>N. sertifer</i>	64.7		70.6	64.9	63.0	40.0	54.3
<i>N. lecontei</i> vs. <i>N. swainei</i>	41.7		55.0	68.7	53.9	42.9	45.6
<i>N. lecontei</i> vs. <i>P. geniculata</i>	58.6		61.1	61.5	—	—	—
Total number responded.....	252	194***	158	176	182	82	260
Number responded to <i>N. lecontei</i>	124	90	84	106	96	40	134
\bar{X} response to <i>N. lecontei</i>	49.2*	46.4**	53.2	60.2	52.7	48.8	51.5

*Parent vs. $F1 x^2 = 0.63$; $P > .32$.

Parent vs. $F2 x^2 = 5.08$; $P < .02$.

**Parent vs. $F3 x^2 = 1.58$; $P > .16$.

Parent vs. $F8 x^2 = 0.13$; $P > .32$.

Parent vs. $F9 x^2 = 1.26$; $P > .16$.

***Data for parental stock excluding responses to *P. geniculata* necessary for comparison of this stock, with $F3$, $F8$, and $F9$.

TABLE VIII

Percentage responses to *D. hercyniae* during paired-species tests with *D. bohémica* from successive generations reared on *D. hercyniae*

Test	Responses to <i>D. hercyniae</i> , %			
	Parent	<i>F1</i>	<i>F2</i>	<i>F3</i>
<i>D. hercyniae</i> vs. <i>N. lecontei</i>	56.8	75.0	59.3	68.7
<i>D. hercyniae</i> vs. <i>N. sertifer</i>	68.4	72.0	76.2	59.3
<i>D. hercyniae</i> vs. <i>N. swainei</i>	69.2	73.9	53.7	56.2
<i>D. hercyniae</i> vs. <i>P. geniculata</i>	55.6	76.2		
Total number responded.....	244	190***	178	294
Number responded to <i>D. hercyniae</i> ..	150	120	132	72
\bar{X} response to <i>D. hercyniae</i>	61.5*	63.2**	74.2	59.2
				61.0

*Parent vs. $F1 x^2 = 7.50$; $P < .01$.

**Parent vs. $F2 x^2 = 0.79$; $P > .32$.

Parent vs. $F3 x^2 = 0.14$; $P > .32$.

***Data for parental stock excluding responses to *P. geniculata* necessary for comparison of this stock with $F2$ and $F3$.

An increased degree of preference for *N. swainei* by parasites of the line bred on this host was evident but the increase was small and persisted through only one generation (Table IX). There were no significant differences between the degrees of preference by parasites of the parental stock when compared with the *F1*, *F2* or *F3* generations ($P > .32$, $.08$ and $.08$ respectively). Responses by parasites of the *F2* generation were about 7% higher than that of the parental stock in spite of the fact that the value of chi-square was not significant. There was, however, a significant decrease in response by parasites of the *F3* generation compared with that of the *F2* generation ($P < .02$). This shows that there was an increase in the degree of preference for *N. swainei* by parasites of the *F2* generation.

TABLE IX

Percentage responses to *N. swainei* during paired-species tests with *D. bohémica* from successive generations reared on *N. swainei*

Test	Responses to <i>N. swainei</i> , %			
	Parent	<i>F1</i>	<i>F2</i>	<i>F3</i>
<i>N. swainei</i> vs. <i>N. lecontei</i>	58.3	60.0	53.6	42.9
<i>N. swainei</i> vs. <i>D. hercyniae</i>	30.8	42.3	64.3	12.5
<i>N. swainei</i> vs. <i>N. sertifer</i>	53.1	55.6	58.8	75.0
Total number responded.....	162	128	146	92
Number responded to <i>N. swainei</i>	84	66	86	40
\bar{X} response to <i>N. swainei</i>	51.8*	51.6	58.9**	43.5

*Parent vs. *F1* $\chi^2 = .01$; $P > .32$.

Parent vs. *F2* $\chi^2 = 1.56$; $P > .08$.

Parent vs. *F3* $\chi^2 = 1.69$; $P > .08$.

***F2* vs. *F3* $\chi^2 = 5.39$; $P < .02$.

The degree of preference for the odour of *N. sertifer* by successive generations of parasites reared on this host increased (Table X). There was no significant difference between the degree of preference for *N. sertifer* by parasites of the parental and *F3* generations ($P > .32$). Preferences for *N. sertifer* by parasites of the *F4*, *F5* and *F6* generations were definitely higher than that of the parental stock ($P < .02$, $.03$ and $.01$ respectively).

Influence of Foliage on Host Preferences

The parasites had definite degrees of preference for the odours of the preferred food trees of the sawflies. The responses to each tree species when tested against the pine needle oil standard are given in Table XI. The differences between the responses to the various trees were significant ($P < .04$) with the order of preference being red pine, white spruce, Scots pine, jack pine and Austrian pine. There was no significant difference between the response to Scots pine and jack pine. Austrian pine was definitely the least preferred (Table XI).

TABLE X
Percentage responses to *N. sertifer* during paired-species tests with *D. bohémica*
from successive generations reared on *N. sertifer*

Test	Responses to <i>N. sertifer</i> , %				
	Parent	F3	F4	F5	F6
<i>N. sertifer</i> vs. <i>N. lecontei</i>	37.0	35.3	45.4	48.0	80.0
<i>N. sertifer</i> vs. <i>D. hercyniae</i>	40.7	31.6	62.5	56.0	27.3
<i>N. sertifer</i> vs. <i>N. swainei</i>	25.0	46.9	60.0	46.1	66.7
Total number responded	124	208	58	152	60
Number responded to <i>N. sertifer</i>	46	78	32	76	34
X response to <i>N. sertifer</i>	37.1*	37.5	55.2	50.0	56.7

*Parent vs. F3 $\chi^2 = .01$; $P > .32$.

Parent vs. F4 $\chi^2 = 5.27$; $P < .02$.

Parent vs. F5 $\chi^2 = 4.62$; $P < .03$.

Parent vs. F6 $\chi^2 = 6.31$; $P < .01$.

TABLE XI
Percentage responses of *D. bohémica* to the odours of the food tree of each
sawfly when tested against a standard of pine needle oil

Test	Number responded	Responses to odour of foliage, %
White spruce	26	46.2*
Red pine	38	50.0
Scots pine	52	34.6
Jack pine	36	33.3
Austrian pine	20	10.0

* χ^2 (between trees) = 10.17; $P < .04$.

The order of preference for the four species of sawflies when present on their preferred food trees was determined by totalling the responses of parasites from three generations in the lines reared on *D. hercyniae* and *N. lecontei* (Table XII). This was done in order to reduce the effect of small fluctuations in responses by the parasites.

The order of preference for the four hosts was the same by parasites of both lines, the order being *N. sertifer*, *N. lecontei*, *N. swainei* and *D. hercyniae*. The differences in the degrees of preference for the four hosts were significant in both lines ($P < .005$).

Conditioning and Preferences for Food Trees of the Hosts

The degrees of preference by parasites from successive generations reared on *N. lecontei* for this host when on red pine decreased (Table XIII).

TABLE XII

Selection of host larvae by *D. bohémica* reared on *D. hercyniae* and *N. lecontei* when the larvae were on their preferred food trees

Parasites tested		Host species			
Reared on	Generation	<i>N. sertifer</i>	<i>N. lecontei</i>	<i>D. hercyniae</i>	<i>N. swainei</i>
<i>D. hercyniae</i> ...	F2	33	33	8	7
	F3	28	20	20	17
	F4	23	14	4	14
	Σ*	84	67	32	38
	%	38.0	30.3	14.5	17.2
<i>N. lecontei</i>	F3	132	144	18	94
	F4	42	60	26	52
	F5	74	12	58	32
	Σ**	248	216	102	178
	%	33.3	29.0	13.7	23.9

* χ^2 (between species) = 32.69; $P < .005$.

** χ^2 (between species) = 63.79; $P < .005$.

TABLE XIII

Percentage responses to *N. lecontei* by *D. bohémica* from successive generations reared on *N. lecontei* when four species of larvae were on their preferred food trees

Generation	Number eggs deposited on four species	Eggs deposited on <i>N. lecontei</i> , %
F3	388	37.1*
F4	180	33.3
F5	176	6.8
F8	102	37.2
F9	172	31.4
F10	200	13.0
F15	160	3.7
F16	384	27.6
F17	522	11.5
F18	300	12.7
F19	118	6.8

* χ^2 (between generations) = 293.43; $P < .005$.

Differences in the preferences between the generations were significant ($P < .005$). Fluctuations in the percentage response to *N. lecontei* were evident but the degree of preference for *N. lecontei* became considerably reduced.

The changes in preferences are more clearly seen when the responses by parasites from the generations tested in each year are added. The degrees of preference were:—

Generation	Total number eggs deposited	Number eggs deposited on <i>N. lecontei</i>	% eggs on <i>N. lecontei</i>
F3–F5 (1947)	744	216	29.03
F8–F10 (1948)	474	118	24.89
F15–F19 (1949)	1484	218	14.69

There were significant differences between these groups ($P < .005$) with a progressive decrease in the response to *N. lecontei* by successive generations of parasites reared on this host. Continuous rearing on *N. lecontei* did not increase the degree of preference by *D. bohémica* for the food tree of this host.

Continuous breeding of the parasite on *D. hercyniae* did not increase the degree of preference for the food tree of this host. Responses to *D. hercyniae* by successive generations when the four species of larvae were on their own food trees were:—

Generation	F2	F3	F4
Number of eggs deposited on four species	226	170	110
Eggs deposited on <i>D. hercyniae</i> , %	7.1	23.5	7.2

The differences in the response to *D. hercyniae* were significant ($\chi^2 = 27.4$, $P < .005$). Response by the F4 generation was much lower than that of the F3. There was, therefore, no increase in the degree of preference for *D. hercyniae* on its food tree, as a result of continuous breeding on this host. The results agree with those obtained with parasites reared on *N. lecontei*.

Discussion

Stimuli Involved in Host Selection and Importance of Food Plant of Hosts

D. bohémica has degrees of preferences for the hosts which it attacks. The parasite is influenced by a number of different stimuli that determine the choice of and enable it to find acceptable hosts. These stimuli act in sequence, influencing host searching and host selection as a chain of stimuli. Chains of stimuli have previously been reported by Richardson (15) and by Ulyett (26). The complete series of stimuli are not necessary to induce oviposition by *D. bohémica* in the laboratory but all the stimuli in the chain influence host selection in the field.

The different order of preferences for the four hosts in each series of experiments was evidence of a chain of stimuli. When selection of host larvae was in response to chemotactile stimuli, *N. lecontei* was most preferred. When only the olfactory senses were involved *D. hercyniae* was most preferred. *N. sertifer* was most preferred when the larvae were present on their food trees and the attractiveness of the foliage influenced the selection of hosts by the parasites. Olfactory responses to the food plant of the host, to the host itself, and chemotactile responses to the host are part of the chain of stimuli.

Preferences of the parasites for the food trees of the different hosts was influenced by stimulation of one or more senses in addition to the olfactory one. The order of preference for the four species of trees when present simultaneously with larvae on them was Scots pine, red pine, jack pine and spruce but the

order of preference for the odours of the trees was red pine, spruce, Scots pine and jack pine. Since the degree of preference for *N. sertifer* was low, the presence of these larvae on Scots pine did not explain the high response to this tree. The degrees of preference for the trees by the parasites was apparently influenced by chemical or chemotactile stimuli, as well as olfactory stimuli. This must be added to the list given above.

The importance of the food of the host during the search for hosts by entomophagous insects was referred to on Page 1. The direct influence of the food tree has been demonstrated for *D. bohémica*. A further important fact shown by the present study is that the host that was most preferred when only larvae were involved was not the most frequently attacked when the larvae were on their preferred food trees. The degrees of preference for the food tree of one host species may decrease or mask a high degree of preference for larvae of another host species. The degree of preference for the food plants is of considerable importance in the selection of hosts, unless two or more of them occur on the same species of food tree.

Host Preferences and Conditioning

Parasites continued to show high degrees of preference for the hosts that were most preferred by the parental stock. *D. hercyniae* was the most preferred host of parasites of the parental stock when tested in the olfactometer; *N. lecontei* was most preferred during random assortment tests. When the effect of conditioning to *N. lecontei* was lost there was a correspondingly increased selection of *D. hercyniae*. Among parasites of the line reared on *D. hercyniae*, this species remained as the most preferred host, despite the loss of conditioning to it. Parasites of the line reared on *N. swaini* showed a continuously high degree of preference for *N. lecontei* during tests with assortments of larvae and *D. hercyniae* continued to be most preferred during tests in the olfactometer. When the effect of conditioning to *N. swaini* was lost, the response to *D. hercyniae* increased (Table IX). The changes in preferences which followed deconditioning to *N. sertifer* by parasites of the line developed on this host were similar to those which occurred in the parasites bred on *N. swaini*. Loss of the conditioned effect was, in general, accompanied by increased responses to the hosts most preferred by the parental stock. Preferences shown by parasites of the parental generation did persist but were modified by conditioning in early generations of each line.

The degree of preference for *N. lecontei* by the line of parasites that had developed on this host became lower than that of the parental stock. These changes that followed the loss of conditioning, were temporary (Table III). The species of hosts that were most preferred by the parental stock were also most preferred by the generations (*F27* and *F28*), that followed these changes. Decreased degrees of preference for a preferred host during some generations did not change the basic preferences of *D. bohémica*.

Preamininal conditioning of *D. bohémica* was induced by breeding it on different hosts. Increased preferences of some degree for the host on which development took place occurred in each of the four lines of the parasite. There was no continued cumulative effect of conditioning since continuous breeding on a particular host did not increase the degree of preference beyond that obtained in the early generations. The absence of a cumulative effect of preamininal conditioning is in agreement with results obtained by Thorpe and Jones (25) working with the parasite *Idechthis canescens*, by Thompson and Parker (19) with *Pyrausta nubilalis* and by Crombie (3) with the blow

flies *Calliphora erythrocephala* and *Lucilia sericata*. Results obtained with *D. bobemica* provide further evidence that cumulative conditioning does not occur in several unrelated groups of insects.

Preimaginal conditioning to a particular host species did not increase the selection of that species when present on its food tree. The effect of conditioning to the host was masked by the comparative attractiveness of different trees. The attractiveness of a food tree was not increased by conditioning toward the host which fed on it.

Evidence of conditioning was obtained during tests with random assortments of host larvae and during paired-species tests in the olfactometer. Conditioning became evident more quickly during the random assortment tests than during the olfactometer tests. In three lines out of four (Tables III to X) conditioning became evident one generation sooner during random assortment tests and was apparent through more generations than during olfactometer tests. There was apparently a factor present in the random assortment tests that did not influence results in the olfactometer tests. Only the olfactory senses were involved in the latter whereas chemotactile senses were important in random assortment tests. Conditioning of chemotactic as well as olfactory senses apparently occurred. When both sensory systems were involved the effect of conditioning became apparent more quickly.

Olfactory stimuli alone did not induce oviposition by *D. bobemica*. Olfactory stimuli frequently caused extrusion of the ovipositor but contact with the host was necessary to induce probing and oviposition. This was true of all females whether or not they had had previous opportunity to oviposit. This agrees with the statement by Richardson (15) that "from present knowledge it seems doubtful whether a free living insect can ever be induced to oviposit by means of an odour stimulus alone". Other examples where olfactory attractiveness was not the ultimate stimulus for oviposition by parasites have been reported by Thorpe and Jones (25) and Williams (31). Ullyett (28) found the same to be true of the moth *Ephesia kühniella* Zell. Since olfactory stimuli are not the final stimuli involved, olfactory conditioning would not likely change the degree of preference for different host larvae during random assortment tests unless the degrees of attractiveness of chemotactile stimuli were also influenced by conditioning. This supports the conclusion that conditioning of chemotactile senses occurred.

The duration of conditioning in *D. bobemica* must be considered from two aspects. First, the effect persisted throughout the oviposition period. In this respect it persisted longer than in *I. canescens* (21) or blow flies (3). Secondly, conditioning occurred only in the early generations and was not persistent as found by Craighead (1) and Hopkins (9).

There were differences in the duration of conditioning to each of the four hosts. Conditioning to *N. sertifer* persisted through a greater number of generations than to the three other hosts. Olfactory conditioning to *N. sertifer* persisted through three generations and was still evident when tests with this line were discontinued at the *F6* generation. Olfactory conditioning to the three other hosts was evident in only one generation. Chemotactile conditioning to *N. sertifer* persisted through four generations. Chemotactile conditioning to *D. hercyniae* also persisted for four generations but only one generation to *N. lecontei*. There was no significant degree of chemotactile conditioning to *N. swainei*. Conditioning of both olfactory and chemotactile senses tended to persist longest in the line of parasites conditioned to the least preferred host.

There were differences in the rate of conditioning to each of the four species of hosts. The parasite became conditioned to *D. hercyniae* sooner than to the three other species, conditioning to *N. lecontei*, *N. swainei* and *N. sertifer* following in that order. This order is the same as for the preferences of the parental stock. Conditioning to the most preferred hosts was evident sooner than to the less preferred hosts.

There were differences in the degree of conditioning toward each host species. Since the degree of conditioning to a host was measured by the percentage increase in the preference for that host, the increase as found for each line of the parasite shows the degree of conditioning toward the host on which each line was bred. The percentage increase in the preference for each host during random assortment tests was *N. sertifer* 21, *D. hercyniae* 19, *N. lecontei* 6 and *N. swainei* 6. The percentage increase for each host during paired-species tests was *N. sertifer* 18, *D. hercyniae* 13, *N. lecontei* 11 and *N. swainei* 7. The percentage increase and, therefore, the degree of conditioning to each host was different.

Conditioning as obtained with *D. bohémica* probably plays a part in determining the fate of the parasite in the field. Acceptance of alternate hosts when the preferred host is at a low population level would aid in maintaining the parasite. This has previously been noted by Findlayson (6) who considered that the type of differential host preference described for *Cephalonomia watersoni* may be advantageous to the species in that a secondary host may replace the preferred one in a season or region in which the latter is scarce or absent. Since the preferred host species of most entomophagous insects continuously vary between high and low population levels, the selection of alternate hosts is of considerable importance. The acquisition of temporary conditioning which has been found to occur in several insects, as well as *D. bohémica*, would not only aid survival of the species but tend to return it to its preferred host when the latter again becomes available.

Conditioning and the Formation of Races

The possible importance of preimaginal olfactory conditioning in evolutionary divergence has been discussed by Thorpe and Jones (25) and Thorpe (24). They pointed out that such conditioning might possibly isolate a population over a long period during which physiological modifications of genetic origin could arise. These modifications might be conserved by the ecological barrier, provided by food preferences, until the isolated fraction of the population was no longer likely to be masked in the genetic reservoir of the main population. There are four reasons why conditioning on the basis of the data obtained with *D. bohémica* would be of little importance in the formation of races. First, the effect of conditioning was temporary and the preferences of the parental stock persisted. This does not agree with Craighead's findings (1) nor does it support the Host Selection Principle of Walsh (29) or Hopkins (9). Persistence of the basic preferences is in agreement with observations by Thompson and Parker (19) who found that prolonged isolation of *P. nubilalis* on a nonpreferred host did not change the basic preference. Persistence of the preferences found in the parental stock of *D. bohémica* would greatly reduce the chance of a population becoming isolated by a food preference.

Secondly, conditioning of *D. bohémica* did not restrict the parasites to the host to which they were conditioned. A group of females which responded to the odour of the host to which they were conditioned did not all respond to that odour when tested a second time after a brief interval. Despite the

fact that the group had been conditioned, individuals did not always select the same host in consecutive tests. The likelihood that individuals within a population may select a food medium other than the most preferred, or the host to which they have been conditioned, is borne out by observations of earlier workers. Larson (12) found that *Stator pruinus* Horn oviposited on different species of hosts even in the presence of abundant quantities of the most preferred host or the host in which it had bred. Crombie (3) found that although a population of blow flies became habituated to a previously repellent odour, individuals might still avoid it. Behaviour of this type by *D. bohémica* would prevent isolation as a result of conditioning where alternate hosts were present. The movement of individuals from one species of host to another and the loss of conditioning would prevent the parasite from becoming fixed on the host to which it was conditioned.

Thirdly, the degree of preference for *N. lecontei* by parasites of the line reared on this host changed through a complete cycle (Page 12). If such changes occur in the field, it would reduce the chance of isolation as a result of conditioning.

The fourth reason is that the decrease in the degree of preference for a host below that of the parental stock as occurred in the parasites bred on *N. lecontei* would clearly increase the number of parasites drifting to other hosts and further reduce the likelihood of isolation.

Other Aspects of Conditioning

Among the possible causes of conditioning investigated by other authors and on which the data in the present paper permit comment are contamination (3, 21), habituation (21, 22) and associative and latent learning (3, 22, 23). None of these seem to explain conditioning in *D. bohémica*.

Contamination would influence the selection of hosts if the emerging parasites were subjected to odours from the host carried into the puparium by the mature parasite larvae. Crombie (3) and Thorpe (21) found by using dyed food media that contamination was of little importance in preimaginal conditioning. The data obtained with *D. bohémica* support the conclusions of Thorpe and Crombie but in a different way. Contamination, if effective at all in increasing the preference of the parasite for the host from which it developed, should be equally effective in all generations bred on the same host. This was definitely not the case in *D. bohémica*, as evidenced by the loss of conditioning after a few generations. Further evidence that conditioning was not the result of contamination is that the degree of preference for *N. lecontei* by parasites bred on this host became lower than the degree of preference of the parental stock for this host.

Habituation was defined by Thorpe (22) as an activity of the central nervous system whereby innate responses to mild shock and warning stimuli wane as the stimuli continue for long periods without unfavourable results. This was not the basis of conditioning in *D. bohémica*. All hosts used were attractive to the parasite and did not induce any avoiding reaction. This was most apparent in the absence of the other hosts as evidenced by the results when the odour of each species was tested against a current of odourless air. There were no repellent stimuli toward which they could become habituated.

Associative learning has been considered by Thorpe (22) to include the simplest conditioning or more elaborate forms of trial and error. He describes latent learning as the preliminary learning of an environment as a whole, together with the subsequent ability to select certain parts of the whole for use as guides

or signals for a new motivation. The conditioning obtained in *D. bohémica* is not easily explained by either associative or latent learning. If learning was involved, exposure should have been effective for more than a few generations. One would expect learning of either type to occur in each generation when the exposure was repeated during the preimaginal development of each generation of the parasite. Learning also fails to explain why the degree of preference for a particular host could become lower than the degree of preference by parasites of the parental stock, despite repetition of the conditioning treatment and the continued absence of any repellent effect.

Latent learning may be defined as the association of a new stimulus with a certain favourable environment (3, 22). Conditioning to a certain olfactory or chemotactile stimulus would influence a parasite to select the host that produces the stimulus because it is associated with a previous favourable host. In the case of *D. bohémica* each of the four hosts was favourable to development. The olfactory response by parasites of the parental stock to all four hosts was high when each was tested against a current of odourless air. All species were readily attacked by these parasites and survival was not significantly different. One would expect that the olfactory and chemotactile stimuli from each species would be an equally strong signal for association with a favourable environment. This was not the case since the degree, rate and duration of conditioning to the four hosts was different. Latent learning does not, therefore, appear to be directly related to conditioning in this species.

Summary

Four lines of a dipterous parasite, *Drino bohémica* Mesn., developed by continuous breeding on different species of sawflies possessed varying degrees of preference for both the hosts and the food plants of the hosts. Preference of the parasite for certain plants led to selection of hosts that were not preferred in the absence of the food plants. Exposure of the parasites to the different hosts changed the degrees of preference for them. The changes were effected through the olfactory and chemotactic sense organs. The changes in preference were not cumulative and did not persist, hosts that were selected most frequently by parasites of the parental stock were also selected most frequently by parasites of subsequent generations. There was no increase in the degree of preference for the food plant of the host on which the parasites developed. The degree of preference after exposure to a host appeared to change through a complete cycle. The degree, rate, and duration of conditioning to different hosts varied. Conditioning to preferred hosts became evident sooner than to nonpreferred hosts, whereas conditioning to nonpreferred hosts tended to persist longer. The duration of conditioning of the chemotactile senses was different from that of the olfactory senses. Conditioning was not the result of contamination, habituation or associative or latent learning. It appears that conditioning is of little importance in the formation of races of *D. bohémica*.

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Species of *Lygus*, *Liocoris*, and Their Allies in the Prairie Provinces of Canada (Hemiptera: Miridae)¹

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The *Lygus* complex was treated as a number of genera and subgenera in a recent paper (Kelton, 1955). The genus *Liocoris* Fieber now contains the economically important species, the *pratensis* group, referred to collectively in the literature as the "lygus" bugs.

In the Prairie Provinces of Canada, several species of the *pratensis* group are of economic importance mainly in the growing of alfalfa seed, especially in the north-central agricultural region and in the irrigated areas of the south-west. A review of the names used in dealing with these pests on the Canadian prairies showed that most of them were based on misidentifications, although fortunately the use of the names has been fairly consistent. Such widely recorded and used names of *Lygus pratensis* (L.) and *L. elisus* Van D. have each been used for specimens of another species, and *L. hesperus* Kngt. for those of three other species.

The main purpose of this paper is to provide economic workers with a means for naming species of *Lygus* and *Liocoris* likely to be encountered in control programs, as well as to provide distribution records and data on feeding habits. Extensive collections made during four years at various localities in the Prairie Provinces yielded many species previously unrecorded in this area and provided new breeding and feeding information.

The internal structures of the male and female genitalia provide excellent taxonomic characters, as shown by Wagner (1940, 1947, 1949, 1950), Slater (1950), and Kelton (1955). The most useful characters are the details of the vesica in the male and the sclerotized rings and the posterior wall of the bursa copulatrix in the female.

The characters of the claspers are not very useful in separating the species treated by Knight (1917), particularly those of the *pratensis* group; however, the claspers are readily accessible and in many cases provide information for separating the subgenera and often certain species.

Taxonomy of the *Lygus* Complex

The genus *Lygus* Hahn, 1833, has been divided by various authors into a number of genera and subgenera. The type of the genus, *Lygus pabulinus* (L.), is not, unfortunately, typical of the genus as ordinarily known, but rather resembles species of *Neolygus* in general form and appearance. In the Prairie Provinces, *pabulinus* (L.) and species of *Neolygus* Kngt. represent the genus *Lygus* Hahn. Species of *pulverulentus* (Uhl.) and *utahensis* Moore belong to the genus *Agnocoris* Reut.; *scutellatus* Uhl. to *Orthops* Fieb.; *distinguendus* (Reut.) to *Salignus* Kelton; *approximatus* (Stål) to *Pinalitus* Kelton; and the economic "lygus" bugs to *Liocoris* Fieb. (Kelton, 1955). Three other genera, *Lygidea* Reut.; *Platylygus* Van D., and *Plesiocoris* Fieb., are included in the generic key as they are often confused with the above genera.

¹Contribution No. 3357, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

If the petition "A proposal to use the plenary powers to fix the type species of the Genus *Lygus* Hahn, 1833", by J. C. M. Carvalho, H. H. Knight, and R. L. Usinger, to the International Commission on Zoological Nomenclature is accepted, the following will be effected:-

Lygus Hahn, 1833, containing the type *Cimex pabulinus* L. and the species of *Neolygus* Kngt., will become *Lygocoris* Reut., 1875. *Liocoris* Fieb., 1858, containing the "lygus" bugs of economic importance, will become *Lygus* Hahn, 1833, with *pratensis* (L.) as type.

²Associate Entomologist.

Key to Genera of *Lygus* Complex and Allies in the Prairie Provinces

1. Second antennal segment shorter than head width across the eyes;
short, oval species *Agnocoris* Reuter
- Second antennal segment longer than head width; elongate species 2
2. Frons with a vertical median groove and four or five transverse grooves;
hemelytra brown, with patches of silky pubescence *Salignus* Kelton
- Frons without median groove on frons; hemelytra not as above 3
3. Eye not extending below ventral rim of antennal fossa; eye spherical,
only moderately emarginate on the inner side (Fig. 81); second
antennal segment nearly as thick as first *Lygidea* Reuter
- Eye extending below ventral rim of antennal fossa; eye elliptical,
deeply emarginate on inner side (Fig. 84); second antennal segment
slenderer at the base than the first 4
4. Second segment of hind tarsus shorter than first; dorsum very shiny
and polished, reddish-brown; head nearly horizontal
(Fig. 83) *Platylygus* Van Duzee
- Second segment of hind tarsus longer than first; dorsum pubescent 5
5. Pronotum rugose rather than punctate; hemelytra yellowish-green
with the costal margin pale; tarsal claws sharply angled
(Fig. 88) *Plesiocoris* Fallen
- Pronotum punctate, sometimes very finely; tarsal claws not sharply
angled (Figs. 89, 90) 6
6. Pronotum and hemelytra deeply and coarsely punctate *Liocoris* Fieber
- Pronotum and hemelytra finely and shallowly punctate 7
7. Pubescence on hemelytra suberect; rostrum reaching middle
coxa *Orthops* Fieber
- Pubescence on hemelytra recumbent; rostrum reaching hind coxa 8
8. Rostrum reaching genital segment *Pinalitus* Kelton
- Rostrum shorter, at most extending only slightly beyond hind
coxa *Lygus* Hahn

**Key to Species of *Lygus*, *Liocoris*, and *Agnocoris* in the
Prairie Provinces**

1. Second antennal segment shorter than head width across the eyes 2
- Second antennal segment longer than head width across the eyes 3
2. Males and females fawn-coloured; the pubescence dense, giving the
hemelytra a strong mottled effect *Agnocoris pulverulentus* (Uhl.)
- Males dark reddish-brown; females reddish; pubescence shorter than
above, the mottling less obvious *A. utahensis* Moore
3. Punctures of pronotum fine and shallow, or indefinite 4
- Punctures of pronotum coarse and deep, widely separated 10
4. Basal carina of vertex obsolete at middle, apparent only near the eyes;
elongate, pale-green species *Lygus pabulinus* (L.)
- Basal carina of vertex distinct at middle 5
5. Frons without red markings 6
- Frons with red markings 8
6. Abdomen uniformly green 7
- Side of abdomen red or brown *L. (Neolygus) omnivagus* Knegt.
7. Membrane pale, with a dark median line forming a longitudinal ray,
widened apically *L. (N.) belfragii* Reut.
- Membrane dark, with patches of pale areas *L. (N.) canadensis* Knegt.
8. Tip of tylus black; second antennal segment uniformly green or
yellow *L. (N.) atritylus* Knegt.

- Tip of tylus concolorous with frons, not black 9
9. Disc of pronotum with black dots or rays *L. (N.) communis* Kngt.
Disc of pronotum green or yellow, without black dots or
rays *L. (N.) quercalbae* Kngt.
10. Frons with five or six oblique grooves or striations on each side of
middle as in Fig. 86 (not to be confused with colour markings
simulating grooves) 11
Frons without grooves, but sometimes with colour markings simulating
grooves 12
11. Rostrum extending to middle coxa or slightly beyond; basic colour
green, with brown or black markings; hemelytra with very short
pubescence; mesoscutellum black; length
5.5-6 mm. *Liocoris nigropallidus* (Kngt.)
Rostrum extending to hind coxa or beyond; basic colour reddish-brown,
with long pubescence on hemelytra, pronotum with prominent
humeral angles; length 6-6.2 mm. *L. humeralis* (Kngt.)
12. Scutellum yellow or green with two short dark dashes at middle of
base; lateral dashes absent 13
Scutellum with black or reddish lateral dashes as in Fig. 50 20
13. Mesoscutellum black throughout 14
Mesoscutellum with pale areas at lateral margins; length
5.5-5.8 mm. *L. desertus* (Kngt.)
14. Species green or yellow with brown or black markings 15
Species red or with red markings on hemelytra; cuneus yellow; second
antennal segment 1.2 times as long as head width;
length 5-5.5 mm. *L. rubrosignatus* (Kngt.)
15. Second antennal segment less than 1.35 times as long as head width 16
Second antennal segment over 1.40 times as long as head width 18
16. Cuneus without a black tip; hemelytra practically glabrous, the
pubescence very short; frons with some red;
length 5.5-5.8 mm. *L. borealis* Kelton
Cuneus with a black tip; hemelytra pubescent 17
17. Frons with an inverted V, sometimes diffuse (Fig. 84); jugum, lora,
and gena blackened; femora usually with blackish spots on ventral
surface; length 5-5.75 mm. *L. nigrosignatus* (Kngt.)
Frons without an inverted V; jugum, lora, and gena pale as head;
femora without black spots; length 5.5-6 mm. *L. elisus* (Van D.)
18. Second antennal segment black, 1.6 times as long as head width;
length 5.6-6 mm. *L. atriflavus* (Kngt.)
Second antennal segment yellow or reddish, less than 1.6 times as long
as head width 19
19. Second antennal segment over 1.5 times as long as head width;
pubescence on hemelytra long and dense;
length 5.75-6 mm. *L. hesperus* (Kngt.)
Second antennal segment less than 1.45 times as long as head width;
pubescence on hemelytra short and sparse; length
5.8-6.5 mm. *L. shulli* (Kngt.)
20. Frons with a submedian vitta, often reduced to a line of dots
(Fig. 85) 21
Frons with a median vitta, or an inverted V, or without markings 24

21. Mesoscutellum black; greenish species with irregular brown markings on hemelytra; pubescence very short; length 5.5-5.8 mm. *L. unctuosus* Kelton
 Mesoscutellum red or yellow at lateral margins; brown or reddish species 22
22. Hemelytra dark brown, with patches of pale silvery pubescence (Fig. 93); length 5.5-5.8 mm. *L. plagiatus* (Uhl.)
 Hemelytra reddish without mottling 23
23. Hemelytra shiny, the pubescence short and sparse; markings on head generally reddish; length 5.5-5.75 mm. *L. rufidorsus* Kelton
 Hemelytra pubescent, not shiny; markings on head generally brown; length 5.5-5.75 mm. *L. lineolaris* (Beauv.)
24. Rostrum reaching fifth or sixth abdominal segment; length 5.5-5.8 mm. *L. varius* (Kngt.)
 Rostrum not reaching third abdominal segment 25
25. Mesoscutellum reddish or with pale areas 26
 Mesoscutellum black with no pale areas 27
26. Tibia with oval or triangular "knee spots"; hemelytra reddish, glabrous; length 5.8-6.6 mm. *L. rubroclarus* (Kngt.)
 Tibia with a brown longitudinal stripe extending one-third of the way from base; hemelytra yellowish-brown; length 7-7.6 mm. (Fig. 50) *L. vanduzeei* (Kngt.)
27. Frons with a distinctive pattern (Fig. 87); species dull olive-green to reddish-brown; second antennal segment black, 1.5 times as long as head width; length 6.5-7 mm. *L. robustus* (Uhl.)
 Frons without such pattern 28
28. Frons with an inverted V-shaped mark (Fig. 84) 29
 Frons without an inverted V-shaped mark 30
29. Pale-green, narrow species; second antennal segment less than 1.35 times as long as head width; length 5.6 mm. *L. nigrosignatus* (Kngt.)
 Greenish-brown, or reddish species; second antennal segment more than 1.4 times as long as head width; length 5.8-6.5 mm. *L. shulli* (Kngt.)
30. Pronotum deeply punctate; each hemelytron with a triangular color pattern at apex; cuneus less than 1.3 (males) or 1.1 (females) times as long as head width; length 5.8-6.3 mm. *L. solidaginis* Kelton
 Pronotum regularly punctate; hemelytra without definite pattern; cuneus more than 1.3 (males) or 1.1 (females) times as long as head width; length 6.5-7 mm. (Fig. 51) *L. columbiensis* (Kngt.)

Explanation of Figures

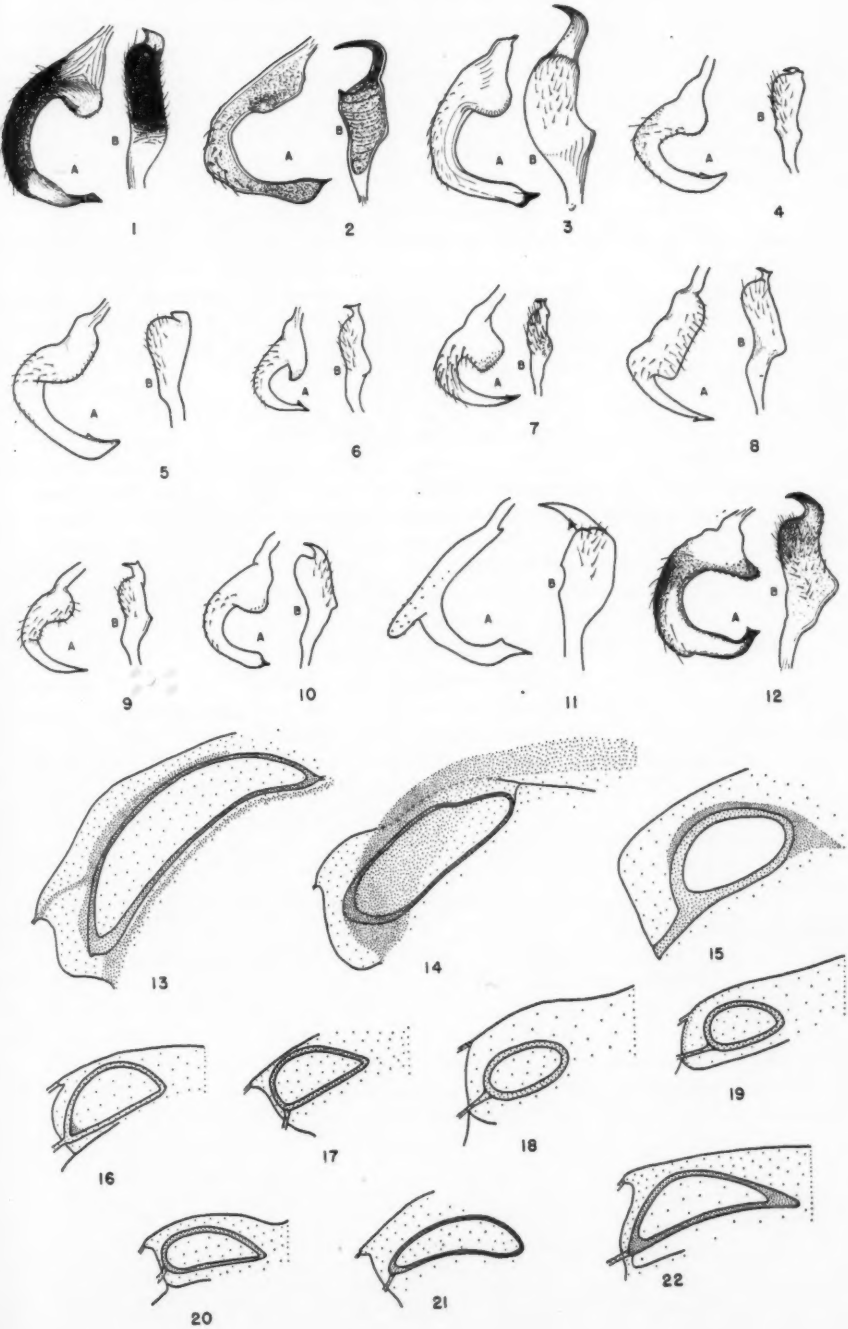
The genital claspers are designated as follows: A, left clasper, dorsal aspect; B, right clasper, ventral aspect.

The sclerotized rings are drawn from the dorsal aspect.

The spicula are drawn from the ventral aspect.

Figs. 1-12. Genital claspers of: 1, *Lygidea salicis*; 2, *Platylygus luridus*; 3, *Plesiocoris rugicollis*; 4, *Agnocoris utahensis*; 5, *A. pulverulentus*; 6, *Orthops scutellatus*; 7, *O. campestris*; 8, *Salignus distinguendus*; 9, *Pinalitus approximatus*; 10, *Lygus* (*Lygus*) *pabulinus*; 11, *Lygus* (*Neolygus*) *communis*; 12, *Liocoris solidaginis*.

Figs. 13-22. Sclerotized ring of female of: 13, *Lygidea salicis*; 14, *Platylygus luridus*; 15, *Plesiocoris rugicollis*; 16, *Agnocoris utahensis*; 17, *A. pulverulentus*; 18, *Salignus distinguendus*; 19, *Pinalitus approximatus*; 20, *Orthops scutellatus*; 21, *O. campestris*; 22, *Lygus* (*Lygus*) *pabulinus*.



Genus *Agnocoris* Reuter, 1875 (*rubicundus* group)

The species are readily recognized by the very short second antennal segment, which is shorter than the head width across the eyes; the brown or reddish colour; the fine punctures on the pronotum and the hemelytra; and the long, dense, recumbent, yellowish pubescence. The genital structures are characteristic (Figs. 4, 5, 15, 17, 52, 53).

The species overwinter as adults.

Prairie species: *Agnocoris pulverulentus* (Uhl.); *A. utabensis* Moore.

Genus *Orthops* Fieber 1858 (*campestris* group)

The species of this genus are recognized by the short oval form; the short, blunt head, which has a distinct and straight basal carina at the vertex; the fine punctures on the pronotum and the hemelytra; and the long, dense, suberect, yellowish pubescence. The rostrum extends to the middle coxa. The genital structures are characteristic (Figs. 6, 7, 20, 21, 56).

The species overwinter as adults.

Prairie species: *Orthops scutellatus* Uhl.

Genus *Salignus* Kelton, 1955

The single species in this genus is readily distinguished by the four or five transverse, black grooves on the frons, at each side of a median, vertical black groove; the dark-brown colour of the hemelytra, with its silvery pubescence that forms pale spots with darker pubescence between; and the fine punctures on the pronotum and the hemelytra. The rostrum reaches the posterior margin of the middle coxae. The genital structures are distinctive (Figs. 8, 18, 54).

The species overwinters as adults.

Prairie species: *Salignus distinguendus* (Reut.)

Genus *Pinalitus* Kelton, 1955

The single species is readily distinguished by the reddish-brown colour; the elongate, narrow form; the finely punctate pronotum and hemelytra; and the long, dense, golden pubescence. The collar is typically white. The rostrum reaches the genital segment. The genital structures are distinctive (Figs. 9, 19, 55).

The species overwinters in the egg stage.

Prairie species: *Pinalitus approximatus* (Stål).

Genus *Lygus* Hahn, 1833 (*Lygocoris* Reuter, 1875)**Subgenus *Lygus* Hahn**

The single species is readily distinguished by the uniform pale-green colour; the elongate, narrow form; the fine punctures on the pronotum and hemelytra; and the long, dense, yellowish pubescence. The genitalia are distinctive (Figs. 10, 22, 57).

The species overwinters in the egg stage.

Prairie species: *Lygus* (*Lygus*) *pabulinus* (L.).

Subgenus *Neolygus* Knight (*communis* group)

The species of this group are recognized by the fine punctures on the pronotum and the hemelytra; the dense pubescence; the relatively long second antennal segment; and, in some species, the colour pattern. The genitalia are characteristic (Figs. 11, 23-28).

The species overwinter in the egg stage.

Prairie species: *Lygus* (*Neolygus*) *communis* Knegt.; *L.* (*N.*) *atritylus* Knegt.; *L.* (*N.*) *canadensis* Knegt.; *L.* (*N.*) *confusus* Knegt.; *L.* (*N.*) *quercalbae* Knegt.; *L.* (*N.*) *belfragii* Reut.; *L.* (*N.*) *omnivagus* Knegt.

Genus *Liocoris* Fieber, 1858 (*pratensis* group)

This is a large and homogeneous group and includes the majority of species encountered in control programs on cultivated crops in the Prairie Provinces.

The species of this group are medium-sized to large and are recognized by the relatively thick body integument and the deep, coarse punctures on the pronotum and the hemelytra. The genital structures are characteristic (Figs. 12, 29-49, 58-79).

The species overwinter as adults.

Prairie species: *Liocoris lineolaris* (Beauv.); *L. hesperus* (Kngt.); *L. elisus* (Van D.); *L. borealis* Kelton; *L. desertus* (Kngt.); *L. rufidorsus* Kelton; *L. varius* (Kngt.); *L. unctuosus* Kelton; *L. columbiensis* (Kngt.); *L. vanduzeei* (Kngt.); *L. rubroclarus* (Kngt.); *L. shulli* (Kngt.); *L. nigrosignatus* (Kngt.); *L. nigropallidus* (Kngt.); *L. humeralis* (Kngt.); *L. plagiatus* (Uhl.); *L. solidaginis* Kelton.

Hosts

The feeding and breeding habits of the species of the *Lygus* complex in the prairie region are very complex. However, the species may be classified into a number of groups according to number of hosts. A number of species occur on single host plants and others on two or more closely related plants, but by far the largest group are miscellaneous feeders on a great variety of plants.

The various groups are as follows:—

Single-host Species

This group contains species that appear to feed and breed on one host plant: *Lygus* (*Neolygus*) *canadensis* Kngt. on American hazelnut, *Corylus americana*; *L. (N.) quercalbae* Kngt. on bur oak, *Quercus macrocarpa*; *Liocoris plagiatus* (Uhl.) on sunflower, *Helianthus* spp.; *L. nigropallidus* (Kngt.) on silvery lupine, *Lupinus argenteus*; *L. varius* (Kngt.) on shrubby cinquefoil, *Potentilla fruticosa*; *L. columbiensis* (Kngt.) on buffalo-berry, *Shepherdia canadensis*; and *L. vanduzeei* (Kngt.) on Canadian goldenrod, *Solidago canadensis*.

Related-host Species

This group contains species that appear to feed and breed on a number of closely related plants: *Lygus* (*Neolygus*) *belfragii* (Reut.) on bush cranberry, *Viburnum* spp.; *L. (N.) atritylus* Kngt. and *L. (N.) omnivagus* Kngt. on dogwood, *Cornus* spp.; *Orthops scutellatus* Uhl. on members of the parsley family, Umbelliferae; *Agnocoris utahensis* Moore, *A. pulverulentus* (Uhl.), *Salignus distinguendus* (Reut.), *Plesiocoris rugicollis* (Fall.), and *Lygidea* spp. on willow, *Salix* spp.; *Pinalitus approximatus* (Stål) and *Platylygus* spp. on members of the pine family, Pinaceae.

Miscellaneous Feeders

This group contains many species that appear to feed and breed on a great variety of plants. Many are pests of economic importance. The habits of *Liocoris borealis* Kelton, a species typical of the *pratensis* group and of major economic importance, may be summarized as follows:— in northern agricultural areas of Saskatchewan the species generally emerges from hibernation in April and early May, and feeds on plants such as bearberry, *Arctostaphylos* sp.; Labrador tea, *Ledum groenlandicum*; and willow, *Salix* spp.; but also alfalfa when available. Farther south the species feeds on willow; snowberry, *Symphoricarpos occidentalis*; and caragana; and moves in May and June to herbaceous plants such as alfalfa; crocus anemone, *Pulsatilla* sp.; and Russian pigweed, *Axyris* sp.; and in June and July to aster, *Aster* spp.; goldenrod, *Solidago* spp.; and wormwood, *Artemisia*, for oviposition. The eggs hatch from

about the middle of June to the end of July, and the nymphs are found until late in the fall, gradually decreasing in numbers throughout September. Egg-laying and hatching appear to occur later on aster, goldenrod, and wormwood than on alfalfa, accounting in part for the greater abundance and later nymphal populations on these plants. Apparently these plants are in more suitable condition for oviposition at the time when the alfalfa plants are fairly mature.

Seasonal Dimorphism

Seasonal dimorphism in colour is most marked in the darker species, and this variation increases the difficulty in naming these species. The hibernating adults of the reddish-brown species are invariably darker and more distinctly reddish than the summer adults, the membrane of the hemelytra is usually light, and the veins are reddish or yellow.³ In the summer adults of these species the general colour of the hemelytra is lighter, the membrane darker, and the veins pale. Different species vary to different degrees. *Liocoris columbiensis* (Kngt.) and *L. solidaginis* Kelton represent one extreme in which the hibernating specimens are very dark reddish-brown to black and the summer specimens are light yellowish-brown. The green species, such as *Liocoris borealis* Kelton and *L. desertus* (Kngt.), are practically unicolorous throughout the year, although the summer specimens occasionally have more extensive darker areas on the head and the hemelytra than the hibernating adults.

Plesiocoris rugicollis (Fall.)

Figs. 3, 15, 82, 88

Phytocoris rugicollis Fallen, 1829: 79.

Plesiocoris rugicollis, Fieber, 1861: 272.

Distinguished by the rugose rather than punctate pronotum, the generally green colour, the sparse black hair on the hemelytra, and the genital structures.

The only previous record of this Palaearctic species in North America is that of Knight (1921) for specimens collected in Alaska.

The species was found breeding on willow, *Salix* spp., in Alberta. The winter is passed in the egg stage.

Specimens examined from:— British Columbia and Alberta. Other records from:— Alaska and Europe.

Agnocoris utahensis Moore

Figs. 4, 16, 52

Agnocoris utahensis Moore, 1955: 178.

Distinguished by the dark reddish-brown colour of the males, the bright red colour of the females, and the forms of the genital structures.

The species breeds on willow, *Salix* spp.

Specimens examined from:— Yukon, Alberta, Saskatchewan, Manitoba, Ontario, and Idaho. Other records from:— Utah, California, and Oregon.

Agnocoris pulverulentus (Uhl.)

Figs. 5, 17, 53.

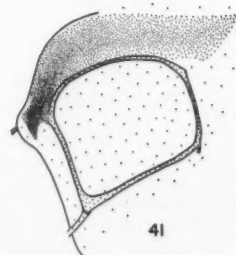
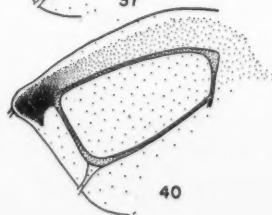
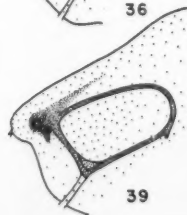
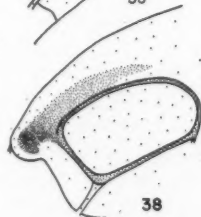
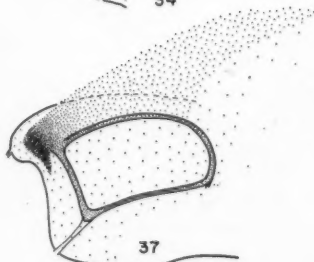
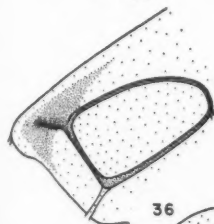
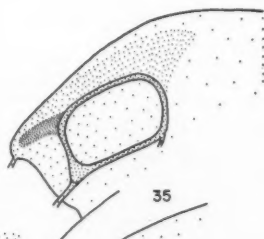
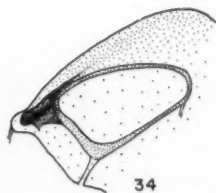
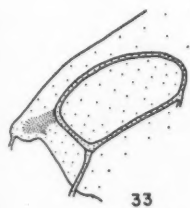
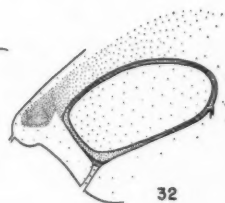
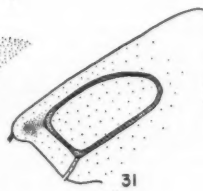
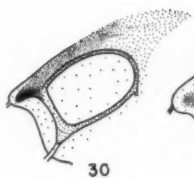
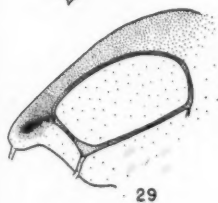
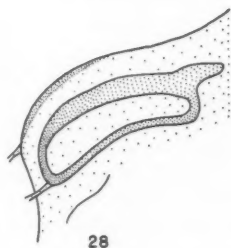
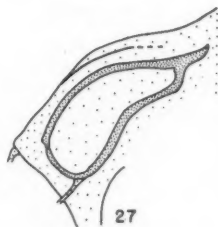
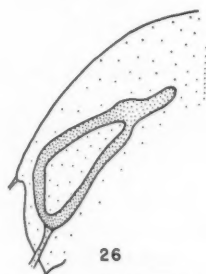
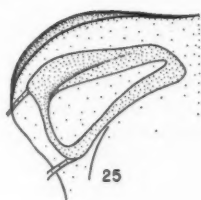
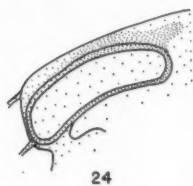
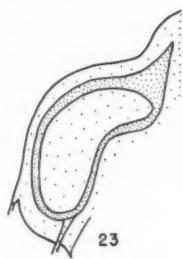
Hadrodema pulverulenta Uhler, 1892: 183.

Lygus rubicundus, Knight, 1917: 589.

Agnocoris pulverulentus, Kelton, 1955: 281.

Distinguished by the brown colour, the dense yellowish pubescence, and the forms of the genital structures.

Figs. 23-41. Sclerotized ring of female of: 23, *Lygus* (*Neolygus*) *communis*; 24, *L. (N.) atritylus*; 25, *L. (N.) belfragii*; 26, *L. (N.) canadensis*; 27, *L. (N.) quercalvae*; 28, *L. (N.) omnivagus*; 29, *Liocoris nigropallidus*; 30, *L. humeralis*; 31, *L. desertus*; 32, *L. elisus*; 33, *L. borealis*; 34, *L. rubrosignatus*; 35, *L. pratensis*; 36, *L. hesperus*; 37, *L. atriflavus*; 38, *L. shulli*; 39, *L. nigrosignatus*; 40, *L. lineolaris*; 41, *L. plagiatus*.



Wagner and Slater (1952) showed that the species found in the eastern United States that was formerly known as *rubicundus* is *pulverulentus* and that *rubicundus* is present in the western United States under the varietal name of *winnipegensis* Kngt. Moore (1955) apparently is of the opinion that *rubicundus* does not occur in North America.

The species breeds on peach-leaved willow, *Salix amygdaloides*.

Specimens examined from:— Alberta, Manitoba, Idaho, Iowa, Illinois, and New York.

***Orthops scutellatus* Uhl.**

Figs. 6, 20, 56, 80

Orthops scutellatus Uhler, 1877: 420.

Lygus scutellatus, Wagner and Slater, 1952: 273.

Distinguished by the pallid green colour, the erect pubescence on the scutellum and the hemelytra, and the genital structures.

This Nearctic species was formerly considered conspecific with the European species *campestris* (L.). Wagner and Slater (1952) showed that *campestris* does not occur in North America.

In the Prairie Provinces, the species breeds on water parsnip, *Sium suave*; and water hemlock, *Cicuta* sp. It is known to attack carrots in British Columbia.

The species is generally distributed in North America. Specimens examined from:— British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Idaho, Utah, Iowa, and New York.

***Salignus distinguendus* (Reut.)**

Figs. 8, 18, 54

Lygus distinguendus Reuter, 1875: 544.

Lygus distinguendus var. *taboensis* Knight, 1917: 587.

Salignus distinguendus, Kelton, 1955: 283.

Distinguished by the dark-brown colour of the hemelytra with spots of silvery pubescence, the fine punctures on the pronotum and the hemelytra, the median and transverse grooves on the frons, and the forms of the genital structures.

The species breeds on beaked willow, *Salix bebbiana*.

Specimens examined from:— Alaska, Yukon, British Columbia, Alberta, and California. Other records from:— Siberia, Utah, Colorado, and New Mexico.

***Pinalitus approximatus* (Stal)**

Figs. 9, 19, 55

Deraeocoris approximatus Stål, 1858: 185.

Lygus approximatus, Reuter, 1879: 53.

Pinalitus approximatus, Kelton, 1955: 282.

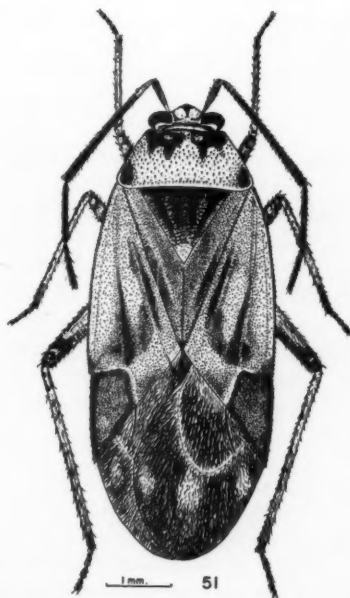
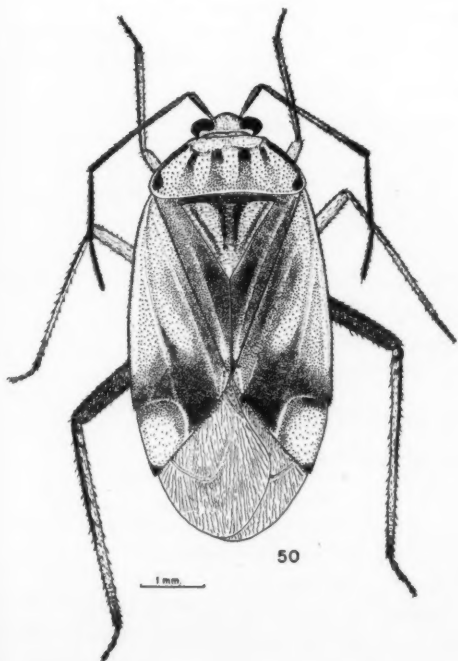
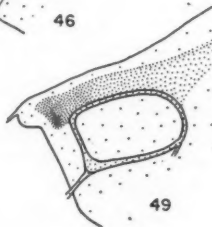
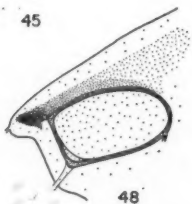
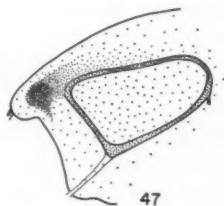
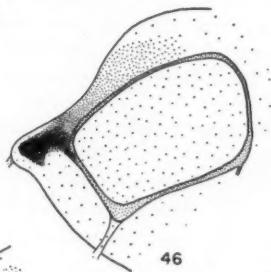
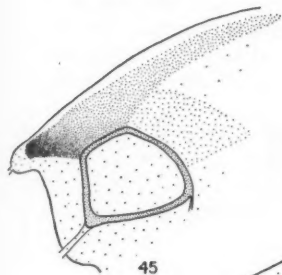
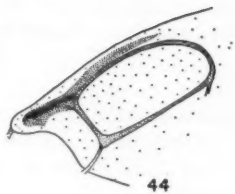
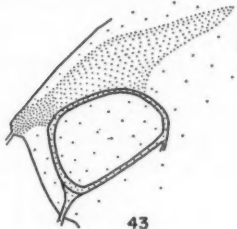
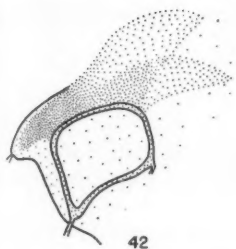
Distinguished by the reddish-brown colour, the fine punctures on the pronotum and the hemelytra, the white collar, the long rostrum, and the forms of the genital structures.

The species was found breeding on spruce, *Picea glauca*, in Alberta; other specimens examined were collected on larch, *Larix* sp., and pine, *Pinus* spp. Knight (1917) collected the adults on goldenrod in New York.

The species appears to be Boreal in distribution in North America. Specimens examined from:— Alaska, Northwest Territories, British Columbia,

Figs. 42-49. Sclerotized ring of female of: 42, *Liocoris rufidorsus*; 43, *L. unctuosus*; 44, *L. varius*; 45, *L. vanduzeei*; 46, *L. rubroclarus*; 47, *L. robustus*; 48, *L. columbiensis*; 49, *L. solidaginis*.

Figs. 50, 51. Adults of: 50, *Liocoris vanduzeei*; 51, *L. columbiensis*.



Alberta, Ontario, Quebec, and New York. Other records from:— Nova Scotia, Maine, and New Hampshire.

***Lygus (Lygus) pabulinus* (L.)**

Figs. 10, 22, 57

Cimex pabulinus Linnaeus, 1761: 253.

Distinguished by the pale-green colour; the elongate, narrow form; the obsolete basal carina at the middle of the vertex, and the forms of the genital structures.

This cosmopolitan species has been recorded as breeding on spotted touch-me-not, *Impatiens biflora*, in New York (Knight, 1917) and the species was collected on this plant in Manitoba. In southern Alberta the species was found breeding on baneberry, *Actaea* sp., the nymphs and adults being collected in July. In July and August the adults were very common on the flowers of cow-parsnip, *Heracleum* sp.

In North America the species appears to have a general distribution. Specimens examined from:—Alaska, British Columbia, Alberta, Manitoba, Ontario, Quebec, New York, and Iowa. Other records from:— Maine, New Jersey, District of Columbia, Maryland, Ohio, North Carolina, and Virginia.

***Lygus (Neolygus) communis* Knegt.**

Figs. 11, 23, 89

Lygus (Neolygus) communis Knight, 1916: 346.

Distinguished by the markings on the head and the pronotum, and the forms of the genital structures.

Dogwood, *Cornus* spp., and holly, *Ilex* spp., are recorded host plants, and the species is also a destructive pest of cultivated pear in New York (Knight, 1917). In the Prairie Provinces it was found breeding on hawthorn, *Crataegus* spp., and was collected on dogwood and willow, *Salix* spp.

Generally distributed in North America. Specimens examined from:— Alberta, Saskatchewan, Manitoba, Iowa, and New York. Other records from:— Idaho, Colorado, Minnesota, Illinois, Maine, Vermont, New Hampshire, Massachusetts, Connecticut, Virginia, and North Carolina.

***Lygus (Neolygus) atritylus* Knegt.**

Fig. 24

Lygus (Neolygus) atritylus Knight, 1917: 606.

Distinguished by the black tip of the tylus, the reddish markings on the head and abdomen, and the forms of the genital structures.

The species breeds on willow, *Salix* spp.

Specimens examined from:— Alberta, Manitoba, and New York. Other records from:— Colorado, Minnesota, Vermont, and New Hampshire.

***Lygus (Neolygus) confusus* Knegt.**

Lygus (Neolygus) confusus Knight, 1917: 606.

No specimens were examined.

Recorded from:— Alberta, New Hampshire, and Maine.

***Lygus (Neolygus) belfragii* Reut.**

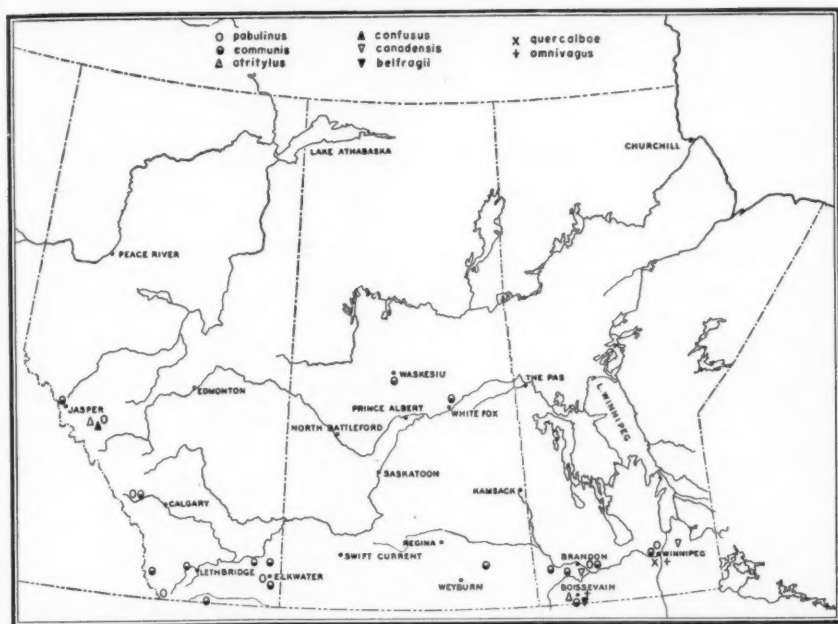
Fig. 25

Lygus belfragii Reuter, 1876: 71.

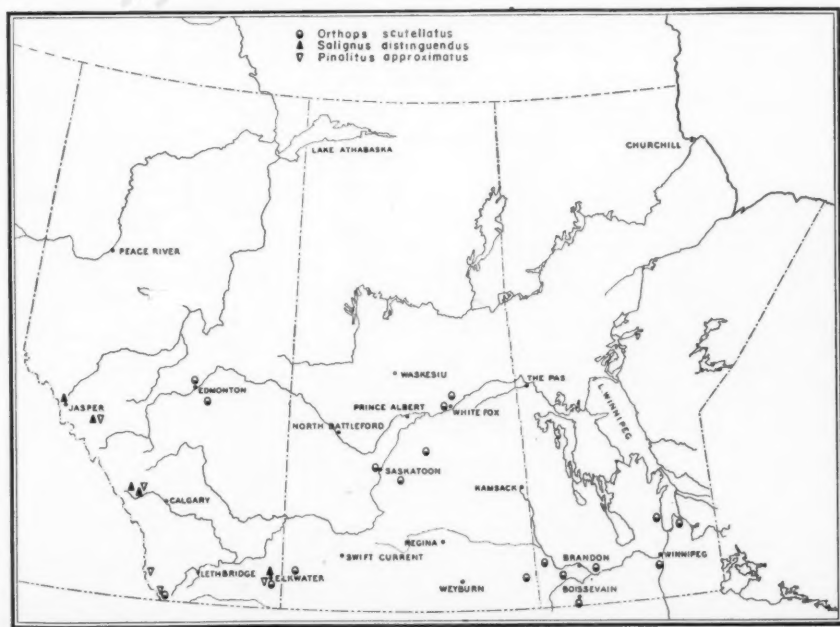
Distinguished by the green colour, the triangular dark patch at the apex of the corium, and the median, longitudinal ray on the membrane.

The species breeds on bush cranberry, *Viburnum* spp.

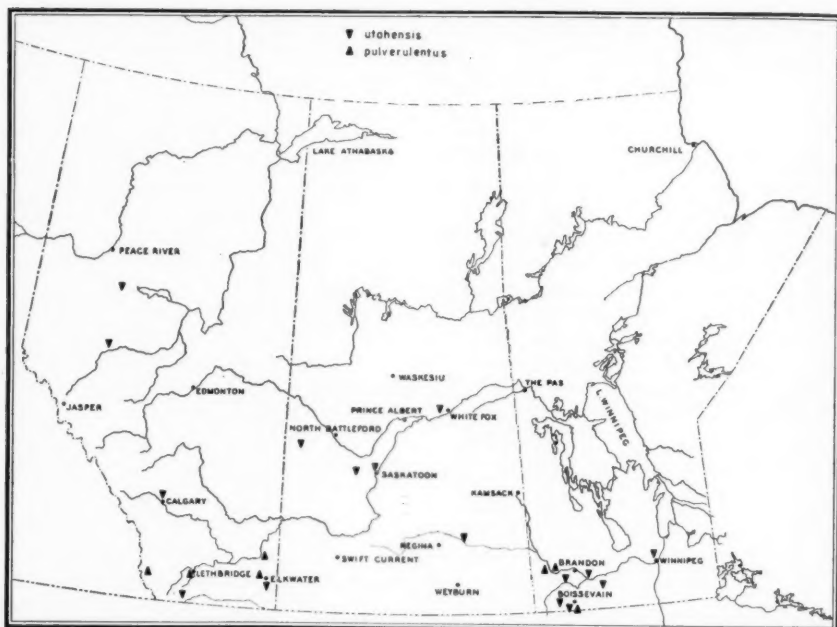
In North America the species appears to have similar distribution to that of *canadensis*. Specimens examined from:— Manitoba and Ontario. Other



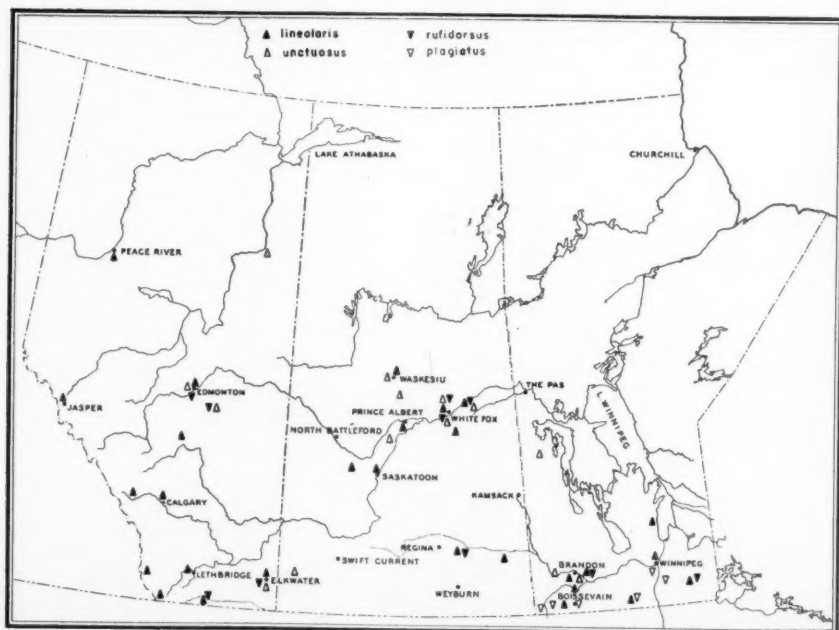
Map 1. Distributions of *Lygus pabulinus*, *L. communis*, *L. atritylus*, *L. confusus*, *L. canadensis*, *L. belfragii*, *L. quercalbae*, and *L. omnivagus*.



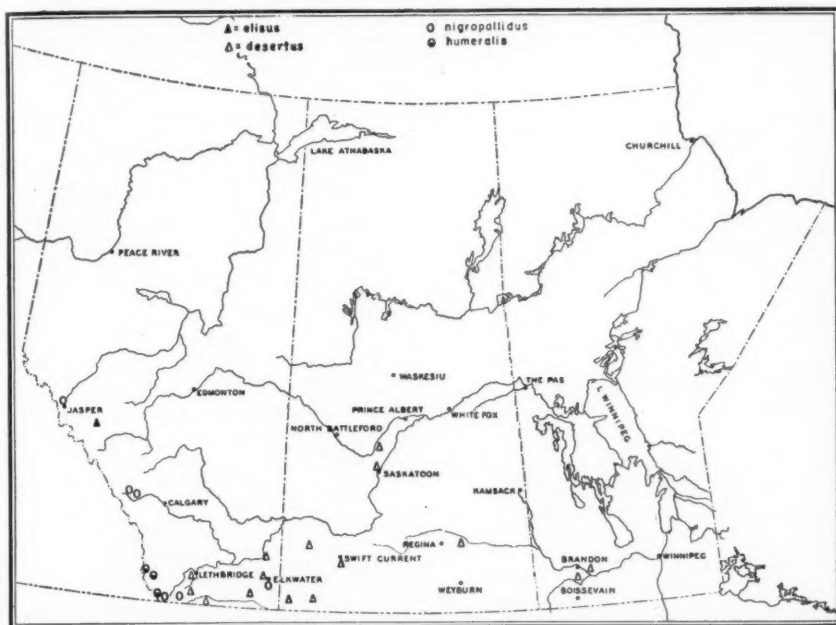
Map 2. Distributions of *Orthops scutellatus*, *Salignus distinguendus*, and *Pinalitus approximatus*.



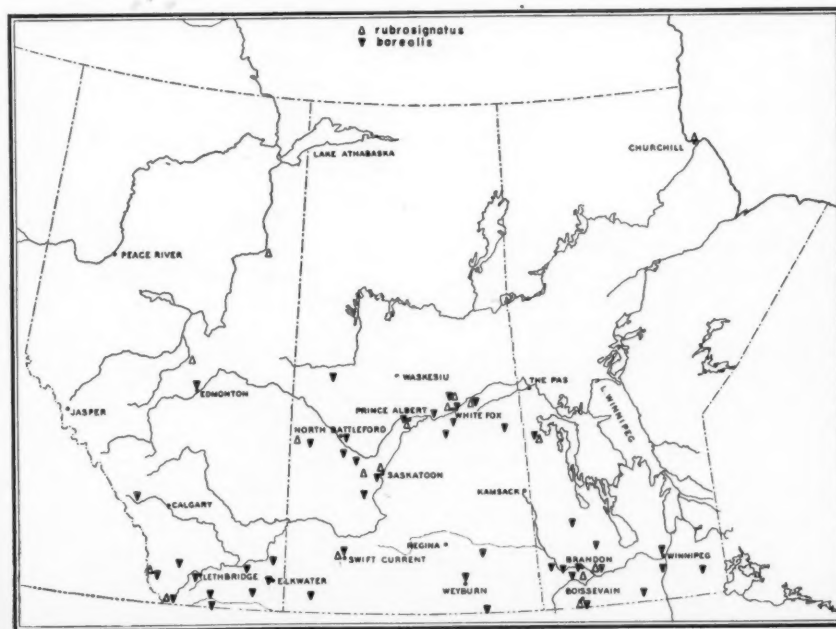
Map 3. Distributions of *Agnocoris utahensis* and *A. pulverulentus*.



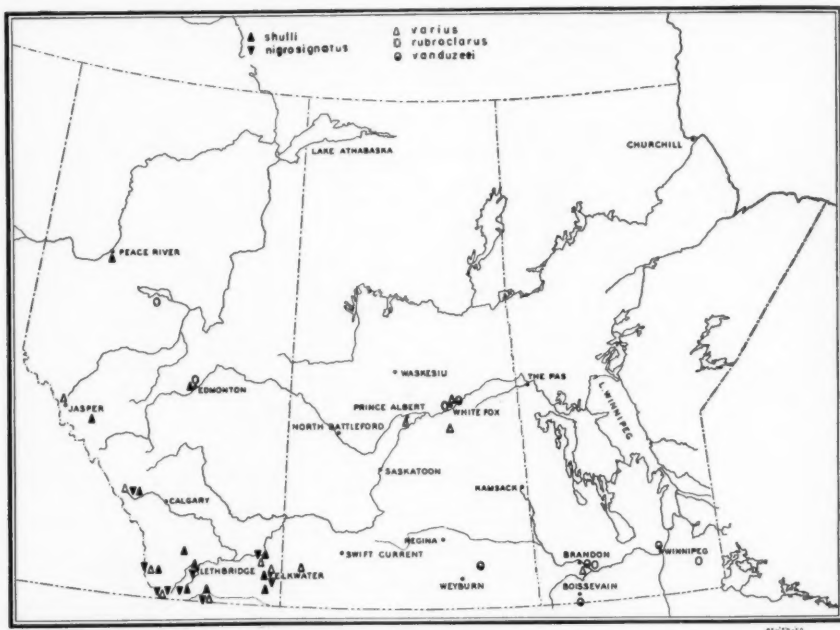
Map 4. Distributions of *Liocoris lineolaris*, *L. unctuosus*, *L. rufidorsus*, and *L. plagiatus*.



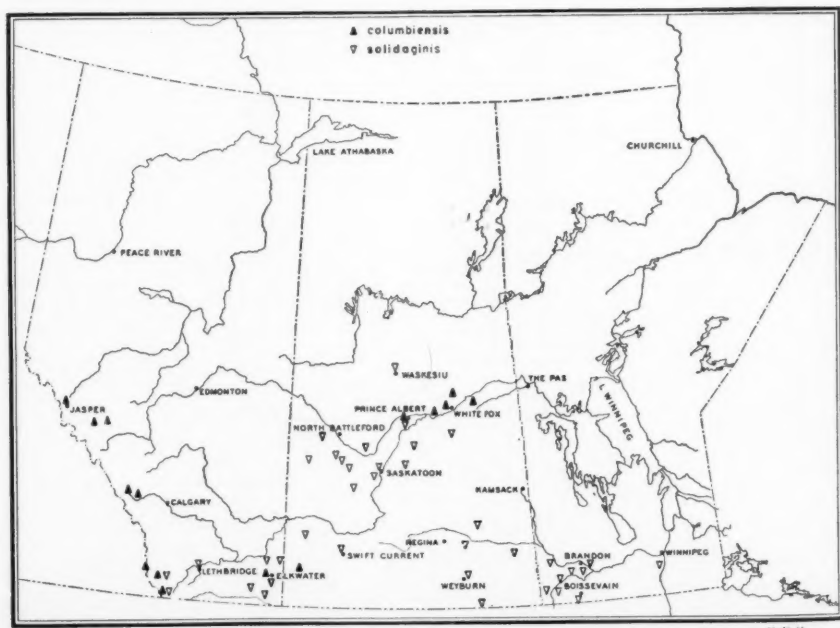
Map 5. Distributions of *Liocoris elisus*, *L. desertus*, *L. nigropallidus*, and *L. humeralis*.



Map 6. Distributions of *Liocoris borealis* and *L. rubrosignatus*.



Map 7. Distributions of *Liocoris shulli*, *L. nigrosignatus*, *L. varius*, *L. rubroclarus*, and *L. vanduzeei*.



Map 8. Distributions of *Liocoris columbiensis* and *L. solidaginis*.

records from:— Minnesota, Wisconsin, Illinois, New York, Maine, and Pennsylvania.

***Lygus (Neolygus) canadensis* Kngt.**

Fig. 26

Lygus (Neolygus) canadensis Knight, 1917: 634.

Distinguished by the red markings of the head, the green abdomen, and the forms of the genital structures.

The species breeds on American hazel-nut, *Corylus americana*.

This species appears to be restricted to North America east of central Manitoba. Specimens examined from:— Manitoba and Ontario. Other records from:— Minnesota, Wisconsin, Illinois, Ohio, New York, and New Jersey.

***Lygus (Neolygus) quercalbae* Kngt.**

Fig. 27

Lygus (Neolygus) quercalbae Knight, 1917: 624.

Distinguished by the reddish markings on the head and abdomen, and the forms of the genital structures.

The species breeds on bur oak, *Quercus macrocarpa*.

In North America the species appears to have similar distribution to that of *belfragii* and *canadensis*. Specimens examined from:— Manitoba and Ontario. Other records from:— Minnesota, Iowa, Missouri, Wisconsin, Michigan, Illinois, New York, Massachusetts, Connecticut, Maryland, and Virginia.

***Lygus (Neolygus) omnivagus* Kngt.**

Fig. 28

Lygus (Neolygus) omnivagus Knight, 1917: 627.

Distinguished by the green frons, the reddish markings on the abdomen, and the forms of the genital structures.

The species breeds on bush cranberry, *Viburnum* spp.

In North America the species appears to have a similar distribution to that of *belfragii*, *canadensis*, and *quercalbae*. Specimens examined from:— Manitoba, Ontario, and New York. Other records from:— Minnesota, Iowa, Wisconsin, Illinois, Michigan, Vermont, Massachusetts, Connecticut, Rhode Island, Pennsylvania, Virginia, and North Carolina.

***Liocoris nigropallidus* (Kngt.)**

Figs. 29, 58

Lygus nigropallidus Knight, 1917: 579.

Distinguished by the pallid green colour, the oblique grooves on the frons, the very short pubescence on the hemelytra, and the short rostrum.

The species breeds on silvery lupine, *Lupinus argenteus*.

The distribution of the species is probably determined by the host plant. Specimens examined from:— British Columbia, Alberta, Montana, Idaho, and Utah. Other records from:— New Mexico and Colorado.

***Liocoris humeralis* (Kngt.)**

Figs. 30, 59

Lygus humeralis Knight, 1917: 570.

Distinguished by the dark reddish-brown colour, the prominent humeral angles of the pronotum, the oblique grooves on the frons, and the dense, yellowish pubescence.

This species appears to be intermediate in form between the short-faced, short-beaked species *nigropallidus*, and the long-faced, long-beaked species *convexicollis*; all three have oblique grooves on the frons.

The life-history of the species is not known.

Specimens examined from:— British Columbia, Alberta, and Utah. Probably widespread in the inter-mountain region of North America.

***Liocoris desertus* (Kngt.)**

Figs. 31, 60

Lygus desertus Knight, 1944: 471.

Distinguished by the green colour, and the pale lateral areas on the black mesoscutellum.

This species is an important pest of alfalfa in the United States and the southern region of the Prairies. It usually is found in association with *lineolaris*, *borealis*, and *shulli*, feeding and breeding on alfalfa, lamb's quarters, *Chenopodium album*; snowberry, *Symphoricarpos occidentalis*; and goldenrod, *Solidago* spp. Salt's (1945) *elusus* probably is this species.

Specimens examined from:— British Columbia, Alberta, Saskatchewan, Manitoba, Montana, Idaho, Utah, Nevada, California, Iowa, and North Dakota. Other records from:— Oregon, Colorado, and Arizona.

***Liocoris elusus* (Van D.)**

Figs. 32, 61

Lygus pratensis var. *elusus* Van Duzee, 1914: 20.

Lygus elusus Van Duzee, 1916: 40.

Similar to *desertus* in the general appearance and the coloration. Separated from *desertus* by the uniformly black mesoscutellum. Separated from *borealis* by the narrower form, the longer pubescence, and the black tip on the cuneus.

This species was erroneously reported from Alberta and Saskatchewan as a pest of alfalfa. Salt (1945) and Bolton and Peck (1946) probably misidentified specimens of *desertus* and *borealis* respectively as of *elusus*.

In addition to attacking alfalfa (Sorenson, 1939; Stitt, 1940), the species is an important pest of beans (Shull, 1933) and cotton (McGregor, 1927) in the United States.

Specimens examined from:— Yukon, British Columbia, Alberta, California, Idaho, and Utah. Other records from:— Wyoming, Colorado, Arizona, Texas, South Dakota, Iowa, Missouri, Minnesota, and Illinois.

***Liocoris borealis* Kelton**

Figs. 33, 62

Liocoris borealis Kelton, 1955: 488.

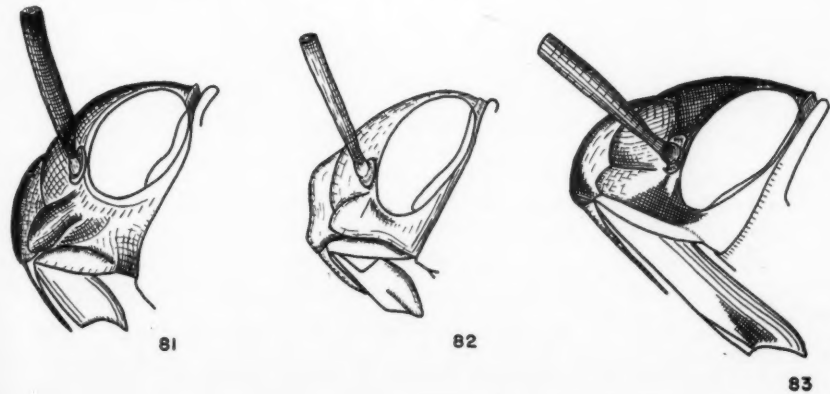
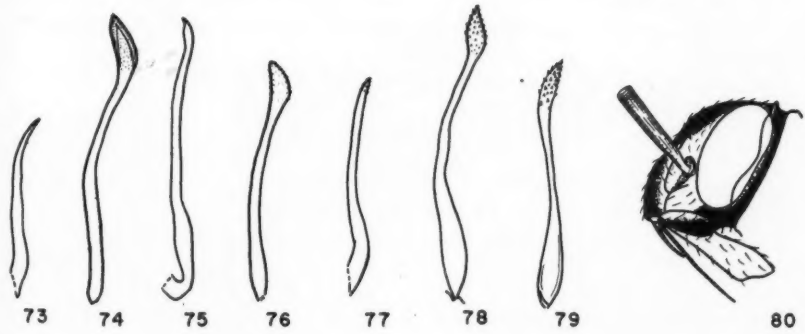
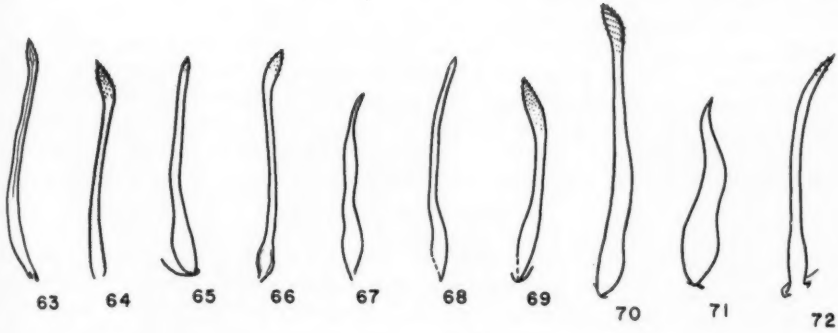
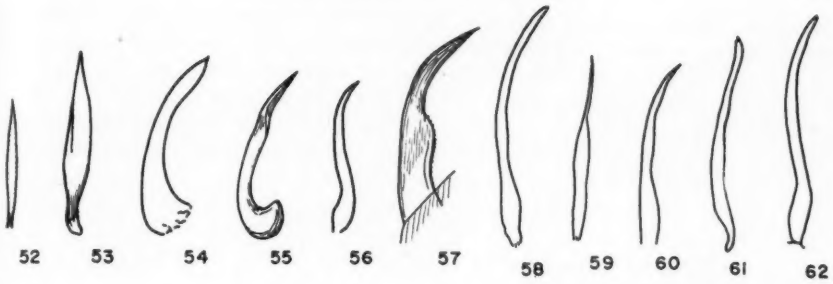
Distinguished by the pale green colour, the red markings on the frons, the short and sparse pubescence on the hemelytra, and usually the absence of a black mark at the tip of the cuneus.

This probably is the species referred to by Knight (1927) as *pratensis*.

The species breeds on a great variety of plants:— alfalfa; aster, *Aster* spp.; goldenrod, *Solidago* spp.; prairie sage, *Artemisia gnaphalodes*; lamb's-quarters, *Chenopodium album*; and snowberry, *Symphoricarpos occidentalis*. Also known to feed on: bearberry, *Arctostaphylos* sp.; Canada thistle, *Cirsium arvense*; bull

Figs. 52-79. Spiculum of the vesica of: 52, *Agnocoris utahensis*; 53, *A. pulverulentus*; 54, *Salignus distinguendus*; 55, *Pinalitus approximatus*; 56, *Orthops scutellatus*; 57, *Lygus pabulinus*; 58, *Liocoris nigropallidus*; 59, *L. humeralis*; 60, *L. desertus*; 61, *L. elusus*; 62, *L. borealis*; 63, *L. rubrosignatus*; 64, *L. pratensis*; 65, *L. hesperus*; 66, *L. atriflavus*; 67, *L. shulli*; 68, *L. nigrosignatus*; 69, *L. lineolaris*; 70, *L. plagiatus*; 71, *L. rufidorsus*; 72, *L. unctuosus*; 73, *L. varius*; 74, *L. vanduzeei*; 75, *L. rubroclarus*; 76, *L. robustus*; 77, *L. columbiensis*; 78, *L. solidaginis*; 79, *L. rutilans*.

Figs. 80-83. Head, lateral view, of: 80, *Orthops scutellatus*; 81, *Lygidea salicis*; 82, *Plesiocoris rugicollis*; 83, *Platylagus luridus*.



thistle, *C. vulgare*; crocus anemone, *Pulsatilla* sp.; cultivated mustard; Labrador tea, *Ledum groenlandicum*; lodgepole pine, *Pinus* sp.; milk-vetch, *Astragalus* spp.; mullein, *Verbascum* sp.; stinkweed, *Thlaspi* sp.; sand dock, *Rumex venosus*; willow, *Salix* spp.; and woolly gromwell, *Lithospermum* sp.

Specimens examined from:— Alaska, Yukon, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Idaho, Montana, Utah, North Dakota, Minnesota, and Iowa.

***Liocoris rubrosignatus* (Kngt.)**

Figs. 34, 63

Lygus pratensis var. *rubrosignatus* Knight, 1923: 576.

Lygus rubrosignatus Knight, 1953: 518.

Distinguished by the generally reddish colour of the hemelytra, the yellow scutellum, and the dense yellow pubescence. The species somewhat resembles *hesperus*, but is smaller in size, with a shorter second antennal segment.

Collected on jack pine, *Pinus banksiana*, and alfalfa in northern Saskatchewan. The adults were collected on ox-eye daisy, *Chrysanthimum* sp., at Carberry, Man.

Specimens examined from:— Northwest Territories, British Columbia, Alberta, Saskatchewan, and Manitoba. Other record from:— Massachusetts.

***Liocoris pratensis* (L.)**

Figs. 35, 64

Cimex pratensis Linnaeus, 1758: 448.

Resembling *hesperus* in the general appearance and pubescence. Separated from the latter by the shorter rostrum and the shorter second antennal segment.

The specimen identified by Knight (1927) as of *pratensis* is probably of the allied Nearctic species, *borealis*. It is doubtful whether *pratensis* occurs in North America.

The species feeds and breeds on a great variety of plants.

It is Palearctic in distribution.

***Liocoris hesperus* (Kngt.)**

Figs. 36, 65

Lygus hesperus Knight, 1917: 575.

Lygus elisus var. *viridiscutatus* Knight, 1917: 575.

Varying in colour from pale green to reddish-brown. Distinguished from allied species by the long, dense pubescence and the long second antennal segment.

This species is an important pest of alfalfa (Sorenson, 1939; Stitt, 1940) and beans (Shull, 1933) in the United States. Salt (1945) probably misidentified specimens of *skulli* for *hesperus*. Bolton and Peck (1946) apparently misidentified specimens of *lineolaris* and *rufidorsus* for *hesperus*.

Specimens examined from:— British Columbia, California, Idaho, and Utah. Other records from:— Oregon, Nevada, Minnesota, Iowa, Michigan, and Illinois.

***Liocoris atriflavus* (Kngt.)**

Figs. 37, 66

Lygus atriflavus Knight, 1917: 572.

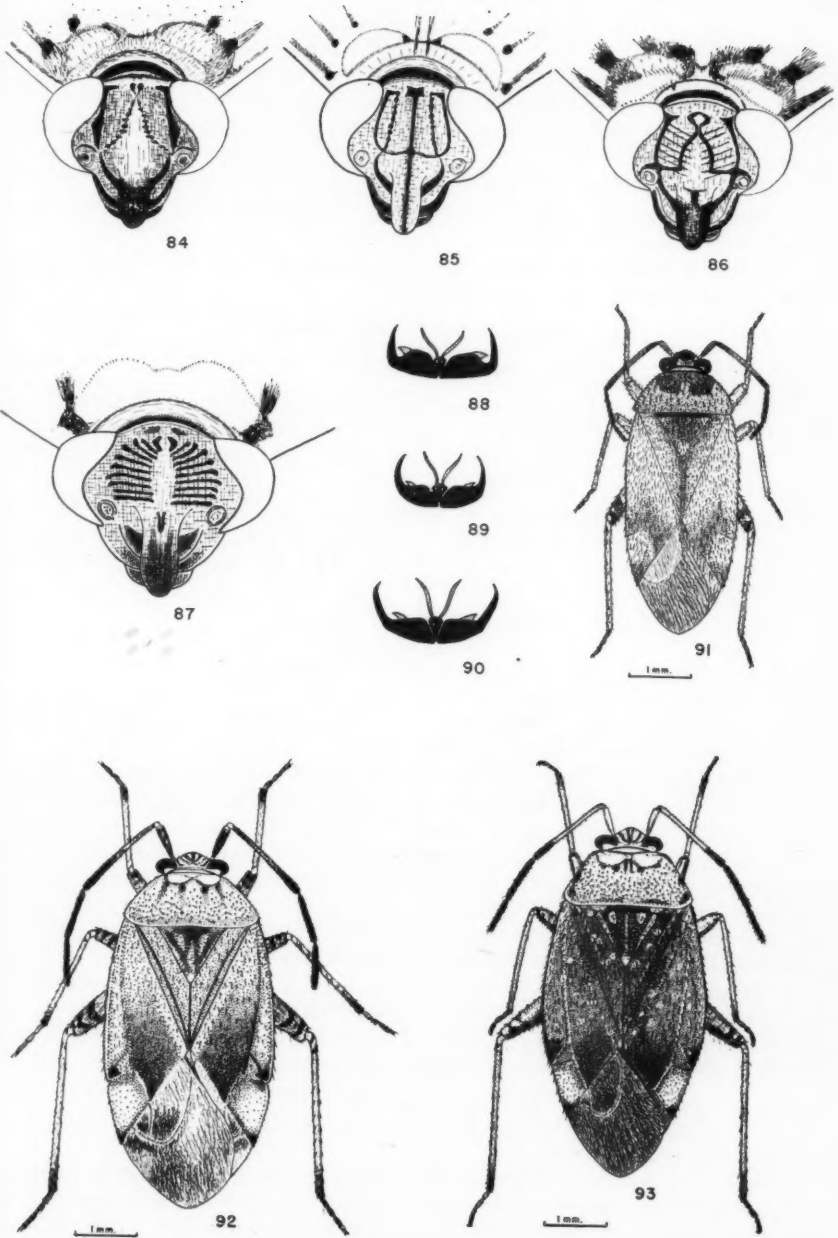
Distinguished by the long, black, second antennal segment.

The life-history of the species is not known.

Figs. 84-87. Head, anterior view, of: 84, *Liocoris nigrosignatus*; 85, *L. lineolaris*; 86, *L. nigropallidus*; 87, *L. robustus*.

Figs. 88-90. Claw of: 88, *Plesiocoris rugicollis*; 89, *Lygus* (*Neolygus*) *communis*; 90, *Liocoris borealis*.

Figs. 91-93. Adult of: 91, *Orthops scutellatus*; 92, *Liocoris lineolaris*; 93, *L. plagiatus*.



Specimens examined from:— British Columbia, Washington, and Idaho. Other records from:— California, Colorado, and New Mexico.

***Liocoris shulli* (Kngt.)**

Figs. 38, 67

Lygus shulli Knight, 1941: 272.

Size and coloration suggestive of *hesperus*, but the shorter pubescence on the hemelytra and the shorter second antennal segment readily separate it from that species.

Salt (1945) probably misidentified this species as *hesperus*.

The species breeds on goldenrod, *Solidago* spp., and Canada thistle, *Cirsium arvense*, and occasionally on alfalfa.

Specimens examined from:— British Columbia, Alberta, Saskatchewan, Washington, Oregon, Idaho, and Utah.

***Liocoris nigrosignatus* (Kngt.)**

Figs. 39, 68, 84

Lygus nigrosignatus Knight, 1941: 270.

Distinguished by the green colour strongly marked with black, the inverted V on the frons, and usually by the double V on the scutellum.

The species strongly resembles *desertus* and *elisus* except for the markings on the frons and scutellum.

At Coutts, Alberta, the species was collected on cultivated mustard. It is also recorded (Knight, 1941) as a pest of alfalfa and peaches in Washington.

Specimens examined from:— British Columbia, Alberta, Washington, Idaho, and Utah.

***Liocoris lineolaris* (Beauv.)**

Figs. 40, 69, 85, 92

Coreus (?) *lineolaris* Palisot de Beauvais, 1805: 187.

Lygus pratensis var. *strigulatus* Walker, 1873: 94.

Lygus oblineatus, Knight, 1941: 148.

Lygus lineolaris, Slater and Davis, 1952: 194.

Distinguished by the reddish-brown or black colour, the median and sub-median vitta on the frons (Fig. 85), the pale or reddish lateral margins of the mesoscutellum, and the black or reddish V's on the scutellum.

This is one of the most abundant of the economic species of *Liocoris* collected in the Prairie Provinces, feeding on a great variety of plants. Species collected on alfalfa, willow, choke-cherry, *Prunus* sp.; caragana; Labrador tea, *Ledum groenlandicum*; stinkweed, *Thlaspi* sp.; lamb's-quarters, *Chenopodium album*; aster, *Aster* spp.; and Russian pigweed, *Axyris* sp.

Specimens examined from:— Alaska, Yukon, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia, Washington, Oregon, California, Nevada, Utah, Idaho, Montana, North Dakota, South Dakota, Minnesota, Iowa, Illinois, Tennessee, and New York.

***Liocoris plagiatus* (Uhl.)**

Figs. 41, 70, 93

Lygus plagiatus Uhler, 1895: 35.

Similar to *lineolaris*, *rufidorsus*, and *unctuosus* in the markings of the head and the scutellum, but differing from those species by the dark-brown colour, the dense pubescence, and the silvery mottling on the hemelytra.

The species was found breeding on sunflower, *Helianthus* spp., in Manitoba.

Specimens examined from:— Manitoba and Iowa. Other records from:— Illinois, Missouri, Massachusetts, Rhode Island, and New Jersey.

***Liocoris rufidorsus* Kelton**

Figs. 42, 71

Liocoris rufidorsus Kelton, 1955: 484.

Distinguished from *lineolaris* by the shorter pubescence on the hemelytra, the longer second antennal segment, and the shorter rostrum. Distinguished from *unctuosus* by the shiny reddish colour, and the pale lateral areas on the mesoscutellum.

This species is usually found in association with *lineolaris*, feeding on alfalfa; bearberry, *Arctostaphylos* sp.; and caragana.

Specimens examined from:— British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Utah, Michigan, and New Hampshire.

***Liocoris unctuosus* Kelton**

Figs. 43, 72

Liocoris unctuosus Kelton, 1955: 486.

Distinguished from species of *lineolaris*, *rufidorsus*, and *plagiatus* by the greasy, brown appearance of the hemelytra, and the uniformly black mesoscutellum.

The species was found feeding on pineapple-weed, *Matricaria matricariodes*, in northern Saskatchewan. It was also collected in association with *lineolaris* and *rufidorsus* on alfalfa; willow; Canada thistle, *Cirsium arvense*; aster; Labrador tea, *Ledum groenlandicum*; and caragana.

Specimens examined from:— Alaska, Northwest Territories, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, and Quebec.

***Liocoris varius* (Kngt.)**

Figs. 44, 73

Lygus varius Knight, 1944: 473.

Resembling specimens of *lineolaris* in size, colour, and pubescence, but differing from that species in the absence of the submedian vitta on the frons and the longer rostrum, which extends to the fifth abdominal segment.

The species breeds on shrubby cinquefoil, *Potentilla fruticosa*.

Specimens examined from:— British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, Labrador, and Utah. Other records from:— Washington, Wyoming, and Colorado.

***Liocoris vanduzeei* (Kngt.)**

Figs. 45, 50, 74

Lygus vanduzeei Knight, 1917: 565.

Distinguished by the large size, the shiny appearance of the hemelytra, the nearly obsolete basal carina at the vertex, and usually by the brown stripe extending down the tibia.

The species breeds on goldenrod, *Solidago canadensis*.

Specimens examined from:— Saskatchewan, Manitoba, Ontario, Quebec, Nova Scotia, New York, and Iowa. Other records from:— Maine, Vermont, New Hampshire, and Massachusetts.

***Liocoris rubroclarus* (Kngt.)**

Figs. 46, 75

Lygus vanduzeei var. *rubroclarus* Knight, 1917: 567.*Lygus rubroclarus* Knight, 1953: 518.

Similar to *vanduzeei* in general appearance, but smaller and lacking the dark stripes on the basal third of the tibia; more reddish in colour, the head with a distinct basal carina at vertex.

The species was collected on alfalfa in the Prairie Provinces.

Specimens examined from:— Alberta, Saskatchewan, Manitoba, Ontario, Quebec, New Hampshire, and Nova Scotia. Other records from:— Maine, Vermont, New Hampshire, and Massachusetts.

***Liocoris robustus* (Uhl.)**

Figs. 47, 76, 87

Camptobrochis robustus Uhler, 1895: 39.

Distinguished by the greenish-brown colour, the design on the frons (Fig. 87), the long and usually black second antennal segment, and the robust size of the species. Resembling species of *atriflavus* in the antenna, species of *unctuosus* in colour and the pubescence, and species of *rubroclavus* in size.

The life-history of the species is not known.

Specimens examined from:— Montana, Idaho, Wyoming, Utah, and Colorado.

***Liocoris columbiensis* (Kngt.)**

Figs. 48, 51, 77

Lygus columbiensis Knight, 1917: 571.

Lygus punctatus, Knight, 1927: 42.

Distinguished by marked sexual and seasonal dimorphism. Males elongate, with a comparatively long cuneus, a small head, and a long second antennal segment; females more robust, with a shorter second antennal segment. Hibernating adults very dark brown to almost black in colour; the cuneus reddish-brown, the membrane pale, the veins reddish. Summer adults yellowish mixed with brown, the cuneus reddish, the membrane fuscous to black, the veins yellow.

Knight (1927) obviously had summer adults of *columbiensis*, which he determined as of *Lygus punctatus* (Zett.) [= *rutilans* Horv.], the latter species not occurring in North America.

The species breeds on Canada buffalo-berry, *Shepherdia canadensis*.

Specimens examined from:— Alaska, Northwest Territories, British Columbia, Alberta, Saskatchewan, and Manitoba.

***Liocoris solidaginis* Kelton**

Figs. 49, 78

Liocoris solidaginis Kelton, 1955: 489.

Distinguished by the deeply punctured pronotum and the hemelytra, the triangular colour pattern at the apex of each corium, and the dense yellowish pubescence.

This species resembles *columbiensis* in general colour, but is readily separated by the distinctive colour pattern on the hemelytra and the longer pubescence.

The species breeds on snowberry, *Symphoricarpos occidentalis*, and golden-rod, *Solidago* spp.

Specimens examined from:— British Columbia, Alberta, Saskatchewan, Manitoba, Idaho, Montana, and Iowa.

Acknowledgments

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The Comparative Internal Larval Anatomy of Sawflies (Hymenoptera: Symphyta)

by

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ABSTRACT

Examination of 132 recognized species of sawflies (Hymenoptera: Symphyta) from America, Europe, Africa, and Australia, has demonstrated the value of internal anatomical larval detail as a taxonomic tool and an indicator of phylogenetic relationship. Two characters, the salivary glands and Malpighian tubules, proved of major importance. The salivary glands fall into three main categories, narrow squared ducts and incorporated gland cells (the Orthandria with the exception of the Xyelidae), narrow ducts and sheathlike gland cells (the Xyelidae), and either increased cell numbers and narrow branching ducts or expanded ducts (the Tenthredinoidea). Three divisions of the Tenthredinidae are suggested, viz. the Selandriinae-Dolerinae-Athaliinae-Lycaotinae, the Nematinae, and the Blennocampinae-Allantinae-Heterarthrinae-Tenthredininae, corresponding to Malpighian tubule groupings of primitive, intermediate-advanced, and advanced. Character trends are discussed in the light of existing adult arrangements (Ross and Benson), and external larval (Yuasa). The survey emphasizes the need of a revision of family and subfamily limits. Where identification is difficult, internal anatomy is of use in determination to genus and species as well as to family and subfamily. The frequency of parallel evolution does not affect the use of certain characters indicative of progressive change within a group.

The Comparative Internal Larval Anatomy of Sawflies (Hymenoptera: Symphyta)¹

By DOREEN E. MAXWELL²

INTRODUCTION

"Few problems in the Hymenoptera have been so disputed as the general classification of the sawfly groups. Practically no two authorities have agreed either on the subject of major groupings, or the basic reason for their division." (52). A wealth of taxonomic literature has accumulated, but it remained for the two foremost authorities in the sawfly field, Benson and Ross, to provide the existing loose framework of sawfly systematics and to point the way to lacunae in knowledge of the group.

As is true of most insect groups, more is known of sawfly adult morphology and taxonomy than of larval structure and classification. Yuasa (69) dealt with external anatomy in the only comprehensive work on sawfly larvae, while internal anatomical details have been generally ignored. Many authorities claim that characters of the immature stages have no phylogenetic importance, a view supporting Comstock's hypothesis that the ontogeny of the larvae is isolated completely from the phylogeny of the race. Ross (52) stated, "On the whole it would appear that the characters affording distinct grouping of the sawfly groups into large segregates, either are not present or have not yet been located in the larvae. It may well be that their characters are adapted to their habits to such an extent as to obscure phylogenetic differences." Yuasa, on the other hand, while acknowledging the danger of mistaking adaptive structures (caenogenetic) for phylogenetic indices, stresses the intrinsic importance of the immature stage in a study of the phylogeny, and justifies this stand in his work. It seemed possible that an examination of the internal anatomy might reveal significant characters useful in corroborating known adult and larval trends.

The investigation was undertaken by the writer to describe and compare the internal anatomy of as many North American species as possible. An attempt was made to correlate such details with the taxonomic schemes outlined by Ross (52) for adults and by Yuasa (69) for larvae. It was found that certain characters did indeed prove fundamental and not directly responsive to environmental conditions; that where identification is otherwise difficult or obscure, internal anatomy may provide a clue not only to family and subfamily but also to genus, and in conjunction with external larval and adult characters even to species; and that the frequency of cases of parallel evolution does not nullify the use of certain characters as indicative of progressive development of the characters within a group. Observations restricted to North American species tend to emphasize apparent relationships and to mask actual phylogenies that might be revealed in a review of world fauna. Advantage was taken of nearly a year spent in Britain to examine European sawfly larvae in many closely related species reared in the Department of Natural History, St. Andrew's University, Dundee, as well as larvae available in the British Museum of Natural History.

MATERIALS AND METHODS

Larval specimens of 11 sawfly families were collected by the writer or obtained through the co-operation of entomological laboratories and museums in Canada, in the United States and in Great Britain. Dissections were carried

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out on preserved specimens and vivisections were performed when living material was available. For drawings the final instar was selected for convenience since enough dissections were made in the various groups of all instars to show that (except in the Cephidae) no major anatomical changes occur during larval growth.

Serial sections, both longitudinal and transverse, were made of the thorax and abdomen of as many species as the supply permitted. Histological results have not been stressed in this account but will be used to emphasize similarities and differences between species, e.g., in cuticular formation, and in the particular characters under comparison, such as the Malpighian tubules and salivary glands.

It was impossible to make all drawings to the same scale without obscuring detail, because sawfly larvae exhibit such extremes in size from species to species. Where possible the figures of species within a family are in proportion and in all cases the relative size at the final instar is indicated on the figure.

In the present work, Ross' (53) system of classification has been used as the basis for the sequence of species. Sawfly material from Europe, Africa, Australia, and South America, not found in his key, has been fitted into his classification according to Benson (4, 7, 8). Specimens supplied and identified by R. B. Benson or H. H. Ross are designated by the initials R.B.B. or H.H.R. after the species name. In all other cases, larval identifications were made by the writer, aided by knowledge of association of larval forms with adults identified by the Unit of Systematic Entomology, Department of Agriculture, Canada; or by use of Yuasa's (69) larval key, and other published or unpublished larval descriptions. The host and locality data refer only to the specimens under study, and no attempt has been made to indicate the range of host plants and distribution of the species.

Figures 1-132, are composite sketches taken from several specimens of individual species, all ventral views. Where the dorsal arrangement and distribution of Malpighian tubules differs from the ventral, diagrammatic sketches are inset, the dotted oval indicating the junction of mid- and hind-gut, the lower edge of the oval, the dorsal surface, the upper edge, the ventral. Lines extending upwards from the oval in the direction of the sketch represent anteriorly-extending tubules, those downwards, posteriorly-extending. The vertical lines delimited by dots, accompanying each sketch, give the relative size of the larvae in question.

Figures 133-147. The letters used and their corresponding terms are as follows:

A.—Abdomen	M.—Muscle
A.R.—Aortic Region	M.G.—Mid-gut
A.M.T.—Anterior region of Malpighian Tubule	M.E.—Mid-gut Epithelium
A.G.—Accessory Salivary Gland (Fig. 123)	M.T.—Malpighian Tubule
A.G.—Abdominal Ganglion (Fig. 124)	N.G.—Nerve Ganglion
A.P.—Abdominal Proleg	O.—Oesophagus (Fig. 123)
B.C.—Basement Cell	O.—Ostium (Fig. 125)
B.M.T.—Bound Malpighian Tubules	O.D.—Oesophageal Diverticulum
C.—Cuticle	O.F.C.—Outer Fat Cells
C.R.—Crypt-like Region	O.V.—Oesophageal Valve
C.C.—Crypt Cell	P.—Pharynx
C.V.—Colic Valve	P.F.—Pericardial Fascia
E.—Epidermis	P.M.—Pericardial Membrane
E.G.—Eversible Gland	P.M.T.—Posterior M.T. Region
F.—Fore-gut	R.—Rectum
F.C.—Fat Cell	R.T.—Rectal Teeth Region
G.—Gonad	S.—Spiracle
G.C.—Gland Cell	S.D.—Salivary Duct
G.O.—Gland Opening	S.G.—Suboesophageal Ganglion
H.R.—Heart Region	T.G.—Thoracic Ganglion
H.E.—Hind-gut Epithelium	T.—Thorax (Fig. 125)
I.F.S.—Inner Fat Sheath	T.—Transverse Muscle (Fig. 124)
I.—Ileum	V.A.S.—Ventral Abdominal Segment
L.—Lumen	
L.G.O.—Lip of Gland Opening	

LITERATURE REVIEW

Taxonomic

Since the time of Linnaeus, a number of schemes for the classification of sawflies has been proposed, the chief differences among them being the relative levels assigned to the various groups. In 1882, Cameron (16) summarized the classifications given by Linnaeus, Leach, Dahlborn, Hartig, and Westwood, and in his own classification divided the sawflies into four families: Tenthredinidae, Cephidae, Siricidae, and Oryssidae. He subdivided the Tenthredinidae into two divisions; I, including the homogeneous Tenthredininae and Nematinae and the distinctly segregated Hylotominae (argids), Cimbicinae, and Lophyrinae (diprionids), and II, the Lydinae (pamphiliids).

Enlarging on a system begun by Thomson (64), Konow (36) in 1905 advocated three family divisions: the Lydidae (pamphiliids, megalodontids, cephids, xyelids, and blasticotomids), the Siricidae, and the Tenthredinidae (cimbicids, argids, diprionids, and tenthredinids). Rohwer (47), in 1911 modified Konow's classification by creating four superfamilies to contain the following groups: the Megalodontoidea (Megalodontidae, Pamphiliidae, Xyelidae, and Cephidae), Orysoidea, Siricoidea, and Tenthredinoidea. In the last group, the argids, pergids, and cimbicids were given family status.

An independent approach was that of MacGillivray (38), who, in 1906, divided the "Tenthredinidae" into nine families: the Xyelidae, Pamphiliidae, Blasticotomidae, Tenthredinidae, Xiphydriidae, Siricidae, Megalodontidae, Cephidae, and Oryssidae on the basis, primarily, of their wing venation. Because of the frequency of parallel evolution in the wing-venation character, his classification at the higher levels, superfamily, family, and subfamily, has been subjected to much criticism, and the validity of his grouping questioned and discarded. However, since progressive development of the wing-venation character within a group seems to provide the best basis of dividing the subfamilies of the Tenthredinidae (52), his analysis and interpretation of 24 subfamilies was a noteworthy contribution.

Yuasa (69), whose classification is based entirely upon external larval morphology, first made a survey to distinguish between environmentally-modified characters and characters of phylogenetic significance. As did Comstock, he recognized two types of phylogenetic characters: one indicative of difference in kind of specialization, the other in degree. From his assembled data, Yuasa pictured a hypothetical larval sawfly ancestor and derived his evolutionary trends from this prototype. It possessed a pair of larvapods on each of the first ten abdominal segments and a pair of segmented subanal appendages on the eleventh. Two distinct stocks arose: in one the larvae possessed larvapods, in the other, subanal appendages. The first evolved into the Xyelidae and Tenthredinidae, the second into the Pamphiliidae, Cephidae, Xiphydriidae, Siricidae, and Oryssidae. Yuasa suggested that the Xyelidae constituted the most primitive family, but that the Pamphiliidae arose from the common stem soon after.

Ross (52) disagreed with Yuasa as to detail but followed a somewhat similar broad classification. His classification is essentially that of Konow, as modified by Rohwer (47), with a few of the more important deviations from the latter being: the elevation of the Cephidae to superfamily rank, the placing of the Oryssidae as a family of the Siricoidea, and the removal of the family Syntectidae from association with the Cephidae into the superfamily Siricoidea. Ross' system, based upon the shape of the head capsule, the mesosternal shape, and the male genitalia, has been accepted by the sawfly zoogeographer Malaise (39) as the one

most nearly expressing the true relationships, as he sees them, in the Tenthredinoidea.

Ross pictured a hypothetical adult Pro-Symphyta as a descendant of the panorpid stem complex, which includes the Neuroptera, Megaloptera, Trichoptera, and Mecoptera. This ancestor had a simple head capsule, distinctive sterno-pleural sutures, slender, multi-segmented antennae, and tibiae with two unmodified apical spines and one to four preapical spurs. Ross established the suborder Symphyta for the sawflies, placing all other Hymenoptera in the suborder Apocrita. The Symphyta are divided into two series, the Strophandria with rotated male genitalia, and the Orthandria with unrotated genitalia. The single superfamily in the Strophandria, the Tenthredinoidea, is believed to have separated from the hypothetical stem at an early stage and given rise first, to the Pergidae, Argidae, Loboceridae, Perreyidae, Pterygophoridae, and Acorduleceridae, and later to the Diprionidae, Cimbicidae and Tenthredinidae. According to Ross, this evolution was possibly correlated with increasing diversity of flora. No archaic group has survived. The Orthandria, remaining initially closer to the hypothetical stem, evolved three distinct super-families whose primitive families are closely linked. These families and superfamilies are the Xyelidae of the Megalodontoidea, Syntectidae of the Siricoidea, and the Cephidae of the Cephioidea. The Megalodontoidea includes the Pamphiliidae as well as the Xyelidae, and Ross stresses that although similar in thoracic structure, legs, and the basic plan of the wings, the two families are remarkably different in head and mouth-parts. Agreeing that the Xyelidae are primitive, Ross would classify them in his main orthandrious grouping farther from the tenthredinid stem than Yuasa places them.

In 1938, Benson (4) surveyed the sawflies as a whole because he believed the time had come to establish an over-all view of world sawfly systematics. He restricted his work to the subfamily level, suggesting tribes and leaving the species-genus approach for a later work (7, 8). Benson's deductions, based as they are on adult and external larval studies, constitute the first attempt at correlating all sawfly groups. His classification is in almost complete agreement with Ross for the Orthandria, with its three superfamilies, Megalodontoidea, Siricoidea, and Cephioidea. The xyelids, however, are given superfamily rank, as the Xyeloidea presumably because Benson finds that the Xyelinae possess strophandrious genitalia as opposed to orthandrious found in all other xyelids. In addition, Benson's description of Australian and South American forms in the Strophandria has emphasized a diversity and complexity hitherto unrealized. Rohwer (47) claimed that "the Pergid Complex" consisted of four families, Perreyidae, Pterygophoridae, Loboceridae, and Pergidae. Ross agreed and added the North American Acorduleceridae. Benson's findings (4) led him to suggest the formation of the family complex, the Pergidae, containing fourteen sub-families and including the acordulecerids.

In 1951, Benson (7) carried his classification to genus and species. In the course of this detailed analysis he incorporated several "radical changes". Thus the dolerines (the Dolerinae of Ross) are considered one of the five tribes of the Selandriinae; the tribe Heptamelini has been transferred from the Heterarthrinae to the Selandriinae; and the subfamily Blennocampinae now includes seven British tribes, among them the Caliroini, Fenusini, and the Emphytini (Allantinae of Ross).

Two morphological studies of the Hymenoptera are noteworthy; Baird's (2) comparative study of the genitalia of Hymenoptera and Taylor's (63) morphology of the tenthredinid head. Taylor reviewed an old controversy as to the Siricidae

being the most primitive sawfly group, and described a developmental trend towards the lapping mouth-parts of higher Apocrita in her work.

Morphological studies have not been the sole contributions to an understanding of the phylogeny of sawflies: Yuasa (69) divides them on the basis of their biology into leaf miners, leaf feeders, web-spinning leaf rollers, borers, and parasites; Ross (52) and Cameron (16) stress the predominance of the leaf-feeding habit in the more primitive sawfly families (exceptions being the occasional leaf miner, fruit miner, and petiole borer), and the combination of biological habits such as leaf-mining at an early instar, leaf-feeding later on.

The nature of cocoons and the place of pupation have been considered of some importance (Ross, 52). Argids and cimbicids have hard cocoons, as have the Nematini and Cladiini, whereas many tenthredinids have weak cocoons or lack them altogether. Megalodontids (free leaf feeders, leaf curlers, feeders in staminate cones, and web spinners) have active pupae, whereas the Siricoidea and Cephoidea borers pupate in wood or stems.

Host relationships have been studied for clues to the problem of origin and direction of evolution in the sawflies. The commonest hosts are the primitive plants, the ferns, conifers, grasses, catkin-bearing trees, and the Rosaceae, whereas few sawflies are found on such higher plants as the Compositae. Some groups are narrowly restricted to their host plants; for example the Diprionidae on conifers, the Selandriinae on ferns, and the genus *Pikonema* on spruce. Cameron (16) provides one of the earliest and most extensive of host-species lists for sawflies, and Benson (6) contributes many interesting points towards a biological phylogenetic study in his host preference details.

The zoogeographical descriptions of the Tenthredinoidea on a world-wide basis, contributed by Malaise (39), are of interest and importance in a determination of phylogenetic trends. It seems evident that in the final analysis it will be only through the collation of the anatomical, biological, and ecological information that the true evolutionary pattern in the sawflies will be determined.

Anatomical

General works on the anatomy and histology of insects were reviewed to provide a background for adult and larval anatomy, first, in different insect orders, second, in the Hymenoptera in general, and, finally, in sawflies in particular.

Three interesting cases of internal anatomical details of taxonomic value were encountered: Rapp's (46) study of Scarabaeoidea showing a phylogenetic trend in the gastric caeca of five subfamilies; Farnsworth's (24) work on the muscles of the head of two mosquito species; and Waterhouse's (66) comparative anatomy of some Mallophaga.

Among the many detailed works available on the Hymenoptera, those by the following proved most valuable: Green (28, 29), Dustan (20), Eastham (21), Gatenby (26), Bugnion (14), Anglas (1), Tiegs (65), Bordas (11), Hering (33), Loele (37), Henschen (32), Pérez (43), Mickey and Melampy (40), and Schneider (57). For the sawflies themselves, Eliescu (22) has written the only fairly complete description of the general internal anatomy of *Lophyrus pini* (*Diprion pini*). He included partial comparative studies of several internal structures in other Diprionidae. There are several references available of special interest as a preliminary to an outline of comparative internal larval anatomy, among them, works by the following: Cholodkovsky (17), Poletajew (45), Frenzel (25), Doncaster (18), Buchner (13), Sanderson (56), Severin (58), Dusham (19), Saint-Hilaire (54), Graber (27), and Holtz (34).

GENERAL ANATOMY OF SAWFLY LARVAE

Sawfly larvae are typically subcylindrical, flattened ventrally to a varying extent and tapering caudally. Specialized forms, such as leaf miners, are conspicuously depressed. The body is well differentiated into a head and three thoracic and ten abdominal segments. Each segment of the body is subdivided in most cases into a number of annulets constant for a species. The larvae possess antennae and three pairs of thoracic legs and may have larvapods on the abdominal segments. Other structures which may be present are a suranal process, a hooklike process on the ultimate tergum, a pair of subanal appendages, and various caudal protuberances and modifications (e.g. extension of anal segments into a rat-like tail). The body may be apparently smooth, spiculate, rough with many protruding glandubae, almost "ciliate" with tall slender bottle-shaped glands, with a slime secretion or scaly bloom, or "armour-plated". For detailed external larval anatomy, Yuasa (69) provides much pertinent information.

A preliminary survey of the internal systems in the various groups was carried out. The nervous, tracheal, muscular, circulatory, and reproductive systems were found grossly similar throughout, and further specific study of these systems was discontinued. It is recognized, however, that detailed differences might be brought out in a thorough study using differential staining techniques.

Differences were readily apparent in the digestive and excretory systems, secretory and general glandular organization, fat body, and body wall. Most of the features are of primary importance in the larval stage. It is in the feeding stage that clues to differentiation, whether primarily environmental or phylogenetic, are likely to be found.

A uniform plan of discussion of larval anatomy was adopted as set forth below:

(A) DIGESTIVE TRACT

1. Fore-gut
2. Mid-gut
3. Hind-gut

(B) MALPIGHIAN TUBULES

(C) SALIVARY GLANDS

(D) FAT BODY

(E) OTHER GLANDS

(F) BODY WALL AND BODY LAYERS

(G) MISCELLANEOUS

To avoid the repetition of headings for every species treated, the letters and numbers given above, will be used.

(A) DIGESTIVE TRACT.

The alimentary canal extends as a fairly straight tube from mouth to anus and is divided into three regions, the fore-, mid-, and hind-gut, which vary in their relative dimensions.

1. *Fore-gut*

The fore-gut extends to about the third thoracic segment in most species and begins as a narrow tube (the pharynx of some authorities) leading from the mouth opening. This tube widens into a pear-shaped oesophagus, which may be so extensible as to form a crop. The oesophagus is constricted near the junction with the mid-gut, which is itself variously folded into a cardiac sphincter. The oesophagus projects into the mid-gut lumen as a circular frilled

envelope, usually lobed, which has been misnamed the oesophageal valve but is merely an oesophageal invagination. This invagination is usually a thin-walled somewhat rigid structure. Wigglesworth (68) gives a description of oesophageal invaginations of various kinds.

Variations are found in the fore-gut. For example, the Diprionidae are characterized by a pair of oesophageal diverticula or pouches which may be short, heavily-muscled structures, or enlarged thin-walled muscular sacs. The crop, if present, is a greatly enlarged, almost transparent extension of the oesophageal epithelium. The Cimbicidae have a further gradation in structure, possessing muscular divisions of the crop region and the fore part of the mid-gut. *Cimbex americana* appears to have a definite muscular proventriculus in the fore-gut.

Histologically the fore-gut consists of a cuticular coat laid down by a thin epidermis resting on the basement membrane, bound by a row of inner longitudinal and outer circular muscles, which are in turn enclosed by connective tissue sheaths. There may be, in some cases, cellular protuberances of the epithelium through the muscle layers into the body cavity. These, thought to be glandular in nature, fit the description provided by Wigglesworth (68) for regenerative crypts, and subsequent reference will be made to them.

2. Mid-gut

The mid-gut has been described by Eliescu (22) in *Lophyrus pini* as possessing three longitudinal protruding folds at the anterior end and extending as a long cylinder to the junction with the hind-gut just posterior to the region of the entrance of the Malpighian tubules. This cylinder he described as being roughly divided into three parts: (1), which is half the length of the mid-gut, possesses muscular foldings; (2), half as long as Part 1, is smooth; and (3), longer than Part 2 but shorter than Part 1, has folds. This description holds generally for *Lophyrus* and the Diprionidae; however, mid-gut divisions (termed regions in the present study), vary greatly in other groups.

The longitudinal folding at the anterior end of the mid-gut is a prominent character in many sawflies, and a different number of folds are to be found, all contributing to the sphincter-like junction with the fore-gut. Longitudinal folds may extend in a straight line or obliquely to the hind-gut, thus presenting a typhlosole-like appearance (*Zaraea*). Gastric caeca are present in several families. In *Arge*, the caeca are located one-third the length of the mid-gut from the anterior end. In *Cimbex*, outpouching caeca are about one-third the mid-gut length from the posterior end. A muscular sphincter, the pyloric valve, separates the mid-gut from the hind-gut. In this region the mid-gut epithelium is thrown into valve-like folds which differ somewhat in various forms.

The peritrophic membrane in a few species appears to extend in as a single sac originating in the region of the oesophageal invagination ("press"). In most forms the membrane is closely applied to the epithelial lining of the mid-gut, and is many layers thick. These layers, it is said, are secreted continuously by the epithelial cells. There is, in most sawflies, probably a double mode of origin for the membrane, secretion from the "press" and from the epithelial cells.

The mid-gut wall is composed of an epithelium of cuboidal to almost columnar cells, thicker than the epithelium of the fore-gut, a basement membrane, and muscle layers (inner circular, outer longitudinal). The mid-gut epithelial cells of insects in general have a striated border, which may be of two types—

one a mobile brush-border of independent hair-like filaments, the other a rod-like border. Sawfly larvae all appear to have a brush-border lining.

The epithelial cells are fairly uniform in shape, differing only in size and degree of elongation, possibly in association with secretion and absorption phenomena. No goblet cells are to be found and there is some question regarding the presence of regenerative cells. Bird (10) has described groups or nidi of small, basal, embryonic or regenerative cells among the large digestive cells of larvae of *Diprion* (*Gilpinia*) *hercyniae*, and stated that there is a certain amount of replacement of old cells along the gut during larval life. The writer has not seen these embryonic nidi in sectioned material of larval stages of *D. hercyniae* and other sawflies. If the observations and interpretation of Bird and the writer are both correct, there may be three types of mid-gut epithelial cells: (1) large, columnar, digestive cells; (2) villi of columnar cells projecting into the body lumen, possibly a type of regenerative crypt; and (3) nidi of basal embryonic cells.

Some sawflies possess a lining thrown into loose, valve-like folds in certain regions. It is noteworthy that in some forms, the Diprionidae and Cimbicidae for example, certain regions of the gut surface have "villi" projecting into the body cavity. These villi, as well as those of the fore-gut, were first interpreted by the writer as having a glandular function. In the Diprionidae they are multicellular, in the Cimbicidae, unicellular, with a crypt connecting with the gut-lumen in each case. Wigglesworth (68) mentions that small basal, embryonic or replacement cells are to be found among active epithelial cells in some insects. These may be scattered singly along the gut or collected at intervals into small groups or nidi, which he described as projecting into the body lumen in "tags".

A controversial issue concerns the type of secretion to be found in sawflies. Secretion is considered to be of two types: holocrine, involving the breakdown of the entire cell in the process and necessitating the presence of replacement cells; and merocrine, where droplets of secretion are manufactured by and extruded from the cell. According to Shinoda (60), the Hymenoptera have a mid-gut reduced in general to the neuropterous type, with nidi seldom well developed except in some adult sawflies. The majority of the Hymenoptera, especially their larvae, he claims show a uniform structure and have purely merocrine secretion. Shinoda describes the orthopterous type of secretion (found in the Orthoptera, Coleoptera, Hemiptera, and Dermaptera) as characterized by an absence of goblet cells and a remarkable development of nidi. The well developed diverticula, indications of the nidi, are so enlarged in certain cases as to appear as caeca. The general epithelial arrangement of some sawfly larvae appears to be strongly similar, in part at least, to this latter orthopterous type. Thus sawflies possibly combine the two types of secretion. Interspersed with the uniform merocrine cells in the Cimbicidae, for example, are these "holocrine nidi" cells, and in the Diprionidae there are definite "holocrine rings" in the region of the fourth abdominal segment. Wigglesworth (68) refers to the adult bee and to *Galleria* larvae as examples of both types of secretion being found together.

The question is, are the regions of the supposed regenerative crypts purely or primarily secretory? It is generally agreed that potentially at least, each mid-gut cell is capable of secreting and absorbing, but it is not known whether phases of absorption and secretion alternate, nor is it clearly understood whether either function is exclusive in any one region. Wigglesworth (67) describes

three regions in detail in the tsetse fly: an anterior region of small, pale cells, absorbing water to make a more "fixable" food medium, a middle, deeply-staining segment secreting digestive enzymes, and a posterior region of narrow cells for absorption. No such divisions have been described for the Hymenoptera in general or the sawflies in particular. As already mentioned, except for slight variations in size and shape the mid-gut cells in sawfly larvae are rather uniform. It is obvious that further work is necessary to explain not only the presence of the crypt-like protuberances of the epithelium into the body cavity but also to clear up the entire question of the phenomena of absorption and secretion.¹

3. Hind-gut

The hind-gut is divided into a slender ileum, a short, bulbous colon, and a large muscular rectum. The colon is valvular and, in certain species, the cuticle contains a ring of spiculate chitinous teeth, the latter being found in a ring in the rectum as well in the same species. Wigglesworth (68) suggests that these teeth serve to pull out the peritrophic membrane from the mid-gut. Eliescu (22) refers to them as chitinous spines arranged in rings. A rectal valve is found in the colon as it enters the rectum, and the latter is divided longitudinally into six rectal pads, which might be glandular (Wigglesworth, 68).

The same three layers are found in the hind- as in the fore-gut, however, the epithelial cells of the latter are smaller and possess a thicker cuticle. In the rectal region, the epithelial cells are larger than in the ileum and the colon, and are arranged along the longitudinal folds. The entire hind-gut is strongly and characteristically muscular.

(B) MALPIGHIAN TUBULES

The Malpighian tubules differ in number and arrangement in the various sawfly groups. Eliescu (22) stated that there are 24 tubules in *Lophyrus*. Each tubule originates on the mid-gut just anterior to its junction with the hind-gut, extends anteriorly a distance one-eighth the length of the mid-gut, then zigzags posteriorly to be tightly bound to the rectum. This condition holds for the Diprionidae but the tubules are not always intimately associated with the rectum but float freely in the posterior body cavity in some species. If associated, there is an arrangement similar to that described for the silkworm by Wigglesworth (68) except that there is usually a single layer of tubes as opposed to a double. Progressive development can be traced in the Malpighian tubules from the condition of few to many tubules opening individually into the mid-gut, to one in which only one or two large main stalks enter after fusion of many or a few tubules.

The structure of a tubule fits Wigglesworth's (68) general description, with a "peritoneal coat of tracheal end-cells, muscles, elastic homogeneous basement membrane, and epithelial cells and cilia". The presence of muscle fibrils is evidenced by the contorted movements in living specimens, and by histological preparations.

A division of labour in Malpighian tubules has been described by Wigglesworth (68). In *Rhodnius* (Hemiptera), for instance, the rod-like border of the epithelial cells in the perirectal absorption area of the tubule gives way to a brush lining in the secretion area near the entrance to the gut.

¹During investigation of the pH of the mid-gut of certain hymenopterous larvae, A. M. Heimpel, Forest Insect Laboratory, Sault Ste. Marie, Ont., found evidence of a variation in pH related to gut morphology, especially in the vicinity of the crypt-like region.

(C) SALIVARY GLANDS

The salivary glands extend as a pair of long, coiled tubes from the pharynx to approximately the beginning of the hind-gut and are surrounded by fat body. A common salivary duct opens to the outside in the region of the mentum of the labium at the sericos. This common duct is short and by branching gives rise to the two main lateral ducts, which may bear accessory glands. Each lateral duct may branch into two or three ducts, which may differ in size. Each duct has a thin epithelial lining with large glandular cells (acini) attached to it. These acini may secrete into the main duct individually by minute ducts or in groups of two or more. The acini may form a complete single-to many-layered ring about the main duct, be distributed in chains along its length, or form numerous grape-like clusters, well separated from it. As will be demonstrated in the specific descriptions, separate functions of secretion by acini and of storage of reserve secretions and transportation by the ducts tend to be consolidated in some groups as acini and ducts fused into compact secreting bodies.

Eliescu (22) mentions three regions in the duct indicative of their secretory and reserve functions. The accessory glands may secrete cementing substances in the anterior region. Further discussion including Saint-Hilaire's (54) description of some sawfly larval salivaries will be found in a subsequent section.

(D) FAT BODY

The so-called fat body is either a loose but definite accumulation of fat cells or a number of scattered ones. Eliescu (22) described the "fat body" in *Lophyrus* as a definite organ consisting of three parts: two strips extending the length of the body from the head to the sixth abdominal segment laterally just under the epidermis, and ventrally around the salivary glands and alimentary canal; a sheath extending from the sixth abdominal segment to the rectum in close association with an enclosing the Malpighian tubules; and a part around the rectum. The parts in the last two regions are thicker than the first, with smaller, more closely packed cells.

Schneider (57) says "the larva is largely an accumulation of reserve materials and is not merely an immature form of the future adult, but has often acquired, quite caenogenetically, a number of adaptations not present in the imago". To Schneider the larval fat body is such an adaptation and is characterized as follows: (1) absence of mitotic divisions in fat cells during post-embryonic life, except in newly-hatched bee larvae (and also in recently-hatched sawfly larvae the writer would add); (2) presence in cells of fat and albumenoids, with the latter formed early in larval life in some species, or not until the last larval instar in other forms; (3) disappearance during metamorphosis of most fat cells by histolysis and possibly phagocytosis; and the retention of others to form an imaginal fat body; and (4) existence in all forms examined in the Hymenoptera, except a torymid, *Monodontomerus*, of separate excretory or urate cells.

Pérez (43) discusses the larval fat body under two headings, the peripheral or external fat-body and the deep fat-body. The peripheral consists of fat cells dispersed in thin clumps, more or less metamerically grouped immediately under the epidermis. The deep fat-body consists of three kinds of cells; true fat cells, urate cells, and oenocytes. These lie grouped into thick folds around the body organs.

The writer found that fat-body distribution in the sawfly larvae in general is not so definite as Eliescu's three-regional effect but is more a deposition of

fat cells around the organs in the body cavity. The presence of separate urate cells is not so common in sawfly larvae as Schneider suggests for the Hymenoptera in general. General dissection and cell study suggest that the female larva possesses a thicker fat sheath than the male.

Oenocytes are frequently found just beneath the hypodermis. They are distinctive because of their pale, clear cytoplasm, darkly staining nucleus, and slightly pyriform shape. Urate cells are distinguishable by their small size, round shape, enlarged nuclei, and position. Leucocyte colonies are distributed throughout the peripheral fat body, especially in the dorsal and ventro-lateral regions.

(E) OTHER GLANDS

Yuasa (69) is one of the few workers to describe glands in the Tenthredinoidea. He mentions that many types of glands opening to the exterior are to be found on various parts of the larvae. Specifically he describes the following: (1) the ventral eversible glands on the ventro-meson of abdominal segments 1 to 7 of the Nematini, Cladiini, and Pseudodoneurini (the scent glands of Benson, 6); (2) the eversible glands in the cervical region of some xyelids; (3) the spiracular glands of *Cimbex*; (4) the wax glands of some Tenthredinidae, such as certain members of the Selandriinae and Allantinae (also described by Dusham (19) in *Macremphytus*); and (5) the cutaneous glands with their sclerotized rings about minute external openings, and other glandubae in the Diprionidae and Tenthredinidae. Stalked glandubae at the end of tubular protuberances are common, and sessile glandubae are found flush with the body surface.

Wigglesworth (68) mentioned glands of internal secretion such as oenocytes and cells of the corpora allata. Glands of Verson (cuticular moulting glands) in sawfly larvae consist of a large main cell and two connected cells. Larvae of the Lepidoptera and Hymenoptera are said to possess a gland in each main tracheal trunk.

No attempt is made to separate, by general description or by suspected function, the various glands encountered in the dissections and sectioning of sawfly larvae. Glands of particular note are the ventral abdominal non-eversible glands of *Arge pectoralis*, the subepidermal glandubae of the Cimbicidae, the sucker-like glands along the sides of Acordulecerinae, and the flask-shaped glands of *Atomacera* and *Sterictiphora* (Argidae).

(F) BODY WALL

The body covering is of great interest not only from a glandular point of view but also from a structural one. There are three cuticular layers secreted by the epidermal cells: the thin epicuticle, the exocuticle, and the endocuticle. The exocuticle and endocuticle are streaked with numerous vertical lines (pore canals of Leydig) whereas the endocuticle possesses horizontal striations (lamellae) as well. Wigglesworth (68) suggests the possibility of extra secretion being laid down by the dermal glands. This would seem a reasonable explanation for the dense "extra-cuticular", shining layer seen in certain sawfly larvae, e.g. *Pikonema alaskensis*. Spicules, spines, and setae may be embedded in any cuticular region or may project from the epidermal region. Various dermal glands open through the cuticle.

(G) MISCELLANEOUS

The typical nervous organization noted in gross dissection consists of a brain, a suboesophageal ganglion, three thoracic and eight abdominal ganglia,

and a double nerve cord. Each ganglion is located approximately midway in a body segment (Fig. 134).

There is a variable number of spiracles. A single pair of pro-thoracic spiracles (thought to have migrated forward) and a pair on each of the first eight abdominal segments are most common. A mesothoracic or metathoracic pair may be present. Two main tracheal trunks run laterally the length of the body with tracheal branches arising from these and ramifying to the organs and all parts of the body.

No attempt is made to discuss the detail involved in sawfly larval musculature but the general organization is depicted (Fig. 134). The gut is bound by muscles; the fore- and hind-gut have inner circular and outer longitudinal layers, the mid-gut the reverse. In all probability a detailed study of musculature would provide evidence of evolutionary change.

The circulatory system consists of a long mid-dorsal cardiac tube extending from the region of the prothorax to the rectum (Fig. 135). The tube is indistinctly divided into a heart with pairs of valved ostia in the abdominal and posterior thoracic regions and the short aorta in the anterior thoracic region. The typical sawfly heart has at least seven pairs of ostia in the abdominal region, each midway in a body segment, a pair of ostia in the third thoracic segment, and a pair in the second thoracic which are closed. The apparently closed aorta turns ventrally and ends at approximately the first thoracic segment. As Wigglesworth (68) describes for *Cloëon* the anterior lips of the valves of the ostia are elongated and meet across the lumen thus preventing the reflux of blood into the heart. Histologically, the heart lining consists of a single cell layer with striated circular muscles applied to this layer. Connective tissue, with penetrating tracheoles, surrounds the lining. The pericardial membrane lies immediately below the heart, attached ventrally and laterally by fan-shaped alary muscle fibres, tracheoles, and its own syncytial cells. As already stated, the pericardial membrane becomes a fascia ventrally in the body.

The gonads, identifiable as ovaries or testes, are found embedded in pockets of fat cells, dorso-laterad of the salivary glands on either side of the alimentary tract, in the posterior part of the fifth abdominal segment. The gonads are connected by ligaments to the dorsal body wall.

ANATOMY OF SAWFLY LARVAE BY SPECIES

SUPERFAMILY MEGALODONTOIDEA

Family Xyelidae

The three species of the Xyelidae examined were so strikingly similar in all internal anatomical details except Malpighian tubules that only *Pleroneura* is described in detail.

Pleroneura borealis Felt. Host, *Abies balsamea* (L.) Mill. Location, Fredericton, N.B., Canada. Fig. 2.

- A. 1. Pharynx, narrow; oesophagus without indication of crop-like expansion. No trace histologically of oesophageal invagination.
2. Mid-gut, fairly wide undifferentiated tube. Histologically gradual transition from tall, cylindrical cells anteriorly, through rectangular cell type, to taller cells near hind-gut junction. "Secretion globules" apparent, cut off from some cells. Thick peritrophic membrane evidently secreted by epithelial cells, its separate, well-defined layers seen between "ciliate" borders of cells themselves.
3. Thick muscular longitudinal folds of rectum extend over colon and ileum. Clear ovoid cells in flaps of colic invagination into rectum.
- B. Ten Malpighian tubules enter mid-gut separately, eight on ventral and ventro-lateral surfaces extending anteriorly, and floating freely in body cavity; two on dorsal surface extending posteriorly and bound perirectally.
- C. Salivary glands, single pair. Each duct enlarged anteriorly into reservoir. Narrows posteriorly, practically surrounded by two compact rows of large square to rectangular salivary gland cells or acini. Each gland cell with individual attachment to duct. Overall effect that of sheath of large gland cells coating duct.
- D. Fat deposition strikingly similar to that of *Cephus cinctus*. Inner "fat body" distributed in compact, bound groups of fat cells. Two fat sheaths bind salivaries, two small "fat bodies" alongside salivary reservoirs. Difference apparent between outer and inner fat cells as Pérez (43) suggests.
- F. Body covering, fairly thick cuticle with occasional embedded spine.

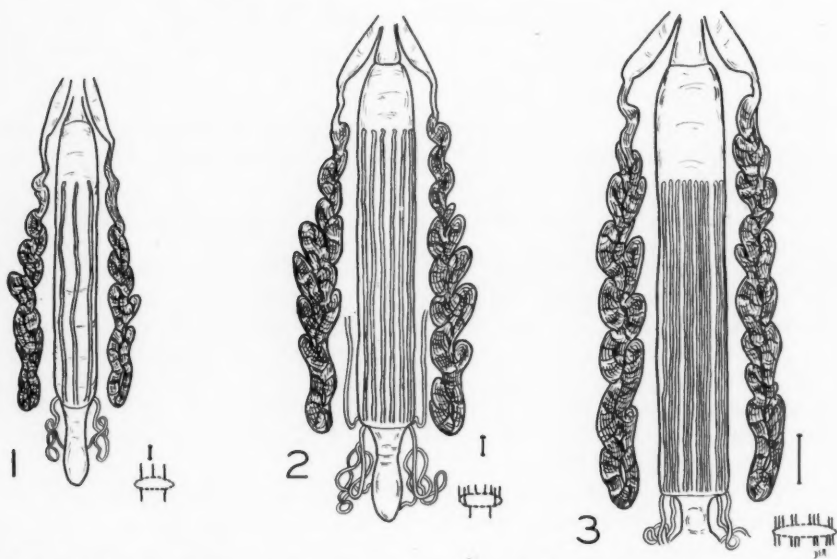
Xyela minor Norton. Host, *Pinus banksiana* Lamb. Location, Sault Ste. Marie, Ont., Canada. Fig. 1.

- B. Five Malpighian tubules enter mid-gut, three ventrally, extending anteriorly, two dorsally, extending posteriorly.

Macroxyela ferruginea (Say). Host, *Ulmus americana* L. Location, Ottawa, Ont., Canada. Fig. 3.

- B. Twenty Malpighian tubules enter mid-gut separately, distributed so that two and three tubules are alternately clumped more closely together. Ten tubules extend anteriorly from the ventral surface of the gut, ten posteriorly from the dorsal.
- E. Lateral eversible cervical glands.

The Xyelidae occupy a most interesting position in sawfly genealogy. Most authorities agree that, on the basis of adult as well as larval characters, this family, attached to "catkin-bearing coniferous or angiospermous trees" (Benson, 4, 7), is, if not the most primitive, at least close to the most primitive to be found.



Figs. 1. *Xyela minor* Norton. 2. *Pleroneura borealis* Felt. 3. *Macroxyela ferruginea* (Say).

Generalized mandibles, open head, preapical spurs, sternopleural sutures, and the unique wing-venation of the adults coupled with the presence of abdominal prolegs on all ten abdominal segments in the larvae, seem overwhelmingly favourable to a theory of their antiquity. Yuasa (69), torn between the Xyelidae (retention of ten pairs of larvapods of the sawfly progenitor) and the Pamphiliidae (retention of ancestral subanal appendages on the "eleventh" segment) as the more nearly representative of postulated ancestral conditions, selected the Xyelidae. Ross (50) describing the five Nearctic genera represented (*Xylecia*, *Xyela*, *Pleroneura*, *Megaxyela*, and *Macroxyela*), stresses the fact that they are markedly distinct, in adult characters at least, more so than any other sawfly group. This, he believes, is an additional proof that the family is ancient. He admits that species limits have not been established within most of the genera.

One of the reasons for including the Xyelidae in the Megalodontoidea, or rather for separating it from the Tenthredinoidea, was Ross' (50) decision that the family was typically orthandrious. Ross (52) omitted specific mention of the male genitalia of the genus *Xyela* in his revision in 1937, and in 1951 Benson (7) separated *Xyela* and *Xyelatana* into a subfamily Xyelinae characterized by strophandrious genitalia as opposed to orthandrious in the rest of the Xyelidae. It is of added interest that Benson (4) described the larvae of the Xyelinae as "with obsolete legs". Although Yuasa (69) mentioned that Dyar had not found larvapods in *Xyela minor*, he characterized the Xyelidae larvae as possessors of 10 pairs. The writer agrees with Dyar's and Benson's findings. In 1938, Benson (4) revised the family on a world basis and created the separate superfamily Xyeloidea. This action places a linking superfamily between the purely orthandrious and strophandrious lines of Ross, a striking confirmation of the theory that places the Xyelidae near the ancestral sawfly.

As stated, the anatomy of the three species described (*Xyela*, feeding on pollen in the staminate cones of *Pinus*; *Pleroneura* feeding on new shoots of *Abies*;

and *Macroxyela*, free leaf-feeder on *Ulmus*) is monotonously similar except for Malpighian tubules and it appears that greater variation is to be found in adults and in larvae externally. Larvae of *Xyela julii* Brébisson (Europe) were examined in England and found to conform in Malpighian tubule number and in general description to *Xyela minor*. More members of the Xyelidae must be examined before conclusions can be drawn as to the validity of Malpighian tubule number and arrangement as characteristic of the species and genus.

In the salivary glands of the Xyelidae, emphasis is placed upon the gland cells rather than upon the duct. The salivaries, on the whole, seem to represent an interesting intermediate between a condition of complete incorporation of the glandular cells into the duct lining with the duct proper subordinated as a gland lumen, as in orthandrious families and of a "free" duct, either narrow in diameter with increased numbers and branching of gland cells, or broad, bordered by small gland cells, in strophandrious families. The presence of reservoirs on the salivary ducts links the Xyelidae with certain more primitive Tenthredinoidea (Strophandria) on the one hand, and with the Orthandria on the other. On the basis of number and arrangement of Malpighian tubules, the Xyelidae are regarded as close to an ancestral form. Accordingly, the arrangement is used as a criterion for the determination of order in the Strophandria as well as for the description of some of the Orthandria. It seems that the creation of a separate superfamily for the Xyelidae (Benson, 7) best expresses the intermediate position its characters indicate between the Orthandria and the Strophandria, a position validated by its anatomy.

Family Pamphiliidae

Acantholyda sp. 2. Host, *Pinus resinosa* Ait. Location, Sault Ste. Marie, Ont., Canada. Fig. 5.

- A. 1. Pharynx and oesophagus, narrow, latter enlarging into wide crop.
2. Anterior part, one-fifth mid-gut length, broadly and deeply longitudinally lobed and thickly transversely muscular. Remainder wide straight tube with faint transverse striations visible to half length of mid-gut.
3. Ileum and colon unmodified. Rectum large. Rectal teeth.
- B. Approximately 20 clumps of Malpighian tubules (2-6 per clump) enter mid-gut. Tubules more closely grouped ventrally (average clump numbers 6,4,4,2,4,4,6) than dorsally (3,6,3,3,2,4,3,4,4,2,6,3), certain variability evident but general pattern consistent. Tubules loop anteriorly, extend posteriorly, bound perirectally.
- C. Salivary glands, one pair main, two pairs of fairly long accessories. Each main duct extends slightly beyond half length of mid-gut, loops anteriorly, bends posteriorly, continuing to approximately beginning of hind-gut. Duct condensed into club-like structure with gland cells in close association, from beginning of posterior bend. General external appearance and histological detail indicate gland cells and duct enclosed within clear sheath forming compact body. Gland cells with individual attachment to slender main duct, form secretory lining about it.
- D. Size difference apparent between inner and outer fat cells. Salivary ducts and gut encased in separate fat-body sheaths. Hind-gut sheath present, as well as rectal abdominal sheath. Fat layers thick in regional distribution, cells interspersed with separate opaque urate cells.
- F. Cuticle extremely thick, histologically similar to that of *Pamphilius* sp.

Acantholyda sp. 1. Host, *Pinus strobus* L. Location, Ottawa, Ont., Canada. Fig. 8.

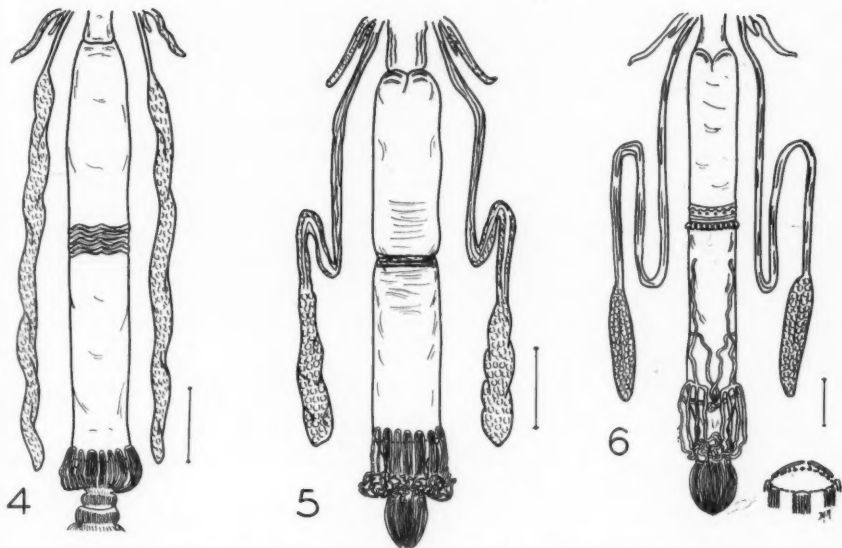
- A 1. Pharynx, narrow; oesophagus, wide, enlarging into broad crop.
2. Anterior part, one-fifth mid-gut length, deeply longitudinally lobed, thickly transversely muscular. Deep transverse striations apparent from one-fifth to almost half. Last six striations raised in transverse bands similar to bands of crypt-like protruding cells in the Diprionidae.
3. Rectum large. Rectal teeth.
- B. Approximately 15 clumps of Malpighian tubules (2-5 per clump) enter mid-gut. Mid-ventrally fairly wide gap in tubule clumping (average clump numbers ventrally 3,4,2,2,4,3 and dorsally 5,3,5,3,3,5,3,5), much more regular arrangement than that of *Acantholyda* sp. 2.
- C. Salivary glands, one pair main, two pairs accessory. Each main duct extends posteriorly about one-third the length of the duct, turns anteriorly, finally extends posteriorly. Cells and duct enclosed within thin sheath from beginning of posterior bend, the whole incorporated into compact body. Cells individually attached to duct.

Cephalcia fascipennis (Cresson). Host, *Picea pungens* Engelm. Location, Sault Ste. Marie, Ont., Canada. Fig. 4.

- A 1. Pharynx, narrow; oesophagus enlarging into good sized crop.
2. First half mid-gut loosely transversely striate. Six pronounced bands at approximately mid-line, similar to those in *Acantholyda* sp. 1, and to the Diprionidae.
3. Large rectum; rectal teeth in lining of colon and rectum.
- B. Approximately eleven evenly-spaced clumps of Malpighian tubules (2-9 per clump), a total of 48 is fairly constant. Tubules tightly bound perirectally, penetrating the rectal outer muscular wall forming an inner and outer layer about the rectal epithelium, as seen in certain Lepidoptera and "Tenthredinids" (Wigglesworth, 68).
- C. Salivary glands, one pair main, one pair accessory. Each main duct extends posteriorly about one-quarter length of entire body. From this point condensed into lightly convoluted club-like structure of salivary-gland cells in close association with it. Cells individually attached to duct.
- D. Size difference apparent between inner and outer fat cells. Separate urate cells interspersed.
- F. Cuticle extremely thick.

Neurotoma fasciata (Norton). Host, *Prunus pennsylvanica* L. f. Location, Ottawa, Ont., Canada. Fig. 6.

- A. 1. Crop, if present, limits indistinct.
2. Anterior edge mid-gut deeply longitudinally scored. Smooth to approximately half length, region delimited by two or three bands of crypt-like cells followed by row of gastric caeca. Remainder smooth.
- B. Two clumps Malpighian tubules enter mid-gut separately dorsally, nine posteriorly directed tubules each clump. Two clumps of two posteriorly extending tubules enter lateral surface. Single stalk enters latero-ventrally each side, swinging ventrally free of the gut. Each stalk sends off one anteriorly directed tubule and four posteriorly directed. Seven posteriorly directed tubules extend from a mid-ventral



Figs. 4. *Cephalcia fascipennis* (Cresson). 5. *Acantholyda* sp. 2. 6. *Neurotoma fasciata* (Norton).

clump, tubules coiling laterally, then posteriorly, where they are bound perirectally.

- C. Similar to salivary glands of *Acantholyda* spp. except ducts double back anteriorly over half extent already traversed posteriorly. From beginning of posterior bend each duct enlarged, beginning of incorporation of gland cells into duct lining in this region. Actual club-shaped end of duct farther posteriorly, definite sheath formed about the gland cells and the duct. Structure of duct in region of bend peculiar histologically, consists of thin core (duct proper) with flattened cellular structure and some nuclei still apparent, a space, followed by a loose transparent sheath or fascia marked faintly by old cell outlines and irregular to dumb-bell-shaped nuclei.
- D. Well-developed fat sheaths present, separate ones about salivary glands. Urate cells scattered among fat cells.

Pamphilus sp. Host, *Prunus nigra* Ait. Location, Ottawa, Ont., Canada. Fig. 7.

- A. 1. Pharynx and oesophagus, narrow, no trace of crop. In histological section, well-developed oesophageal invagination apparent with four full flaps of typically ovoid cells.
2. Mid-gut uniformly slender unmodified tube, delimited anteriorly by deep longitudinal striations. Histologically epithelium shows one of the most interesting modifications to be seen in sawflies. What at first glance appear in sections as round epithelial cells with darkly staining round nuclei are, in reality, sections of inner circular muscles of the sheath about the mid-gut. Cross sections indicate the presence of equally thick longitudinal muscle layers in the valvular region of the mid- and hind-gut junction. The epithelial cells are small, and relatively

uniform, forming a frilly epithelial lining to the mid-gut closely laced by the thick muscular sheath. The gut acts apparently as a rigid muscular tube retaining its appearance as described and its diameter regardless of the presence or absence of food.

The five species of pamphiliids examined all provided with extremely thick muscular binding about the gut, presumably in keeping with the pronounced muscular development in larvae of the Pamphiliidae as a whole, large, powerful forms despite the lack of abdominal prolegs.

- B. Seven main stalks enter mid-gut separately at evenly spaced intervals. Each stalk divides almost immediately into a variable number of tubules (from three to nine). Extremes in variation found were 6, 7, 4, 6, 7, 4, 4 and 6, 7, 3, 9, 6, 3, 3. The tubules extend directly posteriorly and are tightly bound perirectally.
- C. Salivary glands, one pair main, as in *Cephalcia*, two pairs accessory. Main ducts extend as slender tubes approximately to region of second or third abdominal segment. (here gland cells evident for first time) and continue as lightly convoluted club-like structures of cells individually attached to the duct, the whole ensheathed.
- D. Size difference between inner and outer fat cells, urate cells present. Separate extremely thick fat sheaths individually around salivary gland, hind-gut, rectum, and mid-gut.
- F. Cuticle exceptionally thick and lobed, each lobe fan-like from striations in underlying cuticular layers. This pattern traced from epidermal cells well up into the transversely and longitudinally-striate endocuticle. The epidermal cells apparently secrete the shiny cuticular lobe *outside* the epicuticle. In sections, a dense homogeneous haematoxylin-staining layer is superimposed upon ordinary cuticular layers.

The Pamphiliidae have long been regarded as the second most primitive family, next to the Xyelidae, if not the most primitive. As already mentioned, Yuasa (69) claimed that the Pamphiliidae, with their long, 7-segmented antennae, setiferous 3-segmented subanal appendages, setiferous 5-segmented thoracic legs, and well-developed typical mouthparts, is one of the most generalized sawfly families, with larvae differing from the hypothetical larval progenitor only in absence of larvapods and in reduced metaspiracles. The ecology of the larvae, as feeders on Gymnosperms or Angiosperms, whether "solitary" or "colonial" is regarded as fairly specialized. It seemed fairly obvious to Yuasa that, where it was reasonable to assume his "Tenthredinidae" as representing further evolution of the primitive stock from which the Xyelidae evolved, it was equally logical to assume that the Cephidae, Xiphydriidae, Siricidae, and Oryssidae evolved from a stock having the Pamphiliidae somewhere near its origin. Ross (52) stresses the primitiveness of adults and their similarity to the Xyelidae. He points out that few characters have been discovered that divide the groups into definite segregates. As a result, species and genus limits and their possible overlap remain uncertain. Ross (53) did not separate his four genera into subfamilies, in his 1951 revision at least, whereas Benson (7) uses the Cephalciinae for the two genera attached to Gymnosperms and the Pamphiliinae for *Neurotoma* and *Pamphilius*, attached to woody Angiosperms.

Anatomical results do not reveal the supposed primitive nature of the family. The salivary glands, consisting of slender ducts and compact bodies of gland cells incorporated into the duct lining, the whole enclosed in a common sheath, appear intermediate between those of the Xyelidae, on the one hand, and those of the more specialized sawfly families (e.g. the Siricidae), and the Apocrita and "higher" Hymenoptera, on the other. The Malpighian tubule condition is again intermediate, between the author's concept of a generalized arrangement consisting of a low number of tubules entering the gut separately and an advanced one with one or two common stalks to the tubules. Except for a slightly higher degree of specialization in *Neurotoma*, the tubules seem to have attained a developmental level, just above that of the majority of species in the Diprionidae and the Nematinae, through the fusion of several tubules into separate clumps. It remains to be seen whether additional species will show the same relatively homogeneous picture or a greater range in variation.

Table I summarizes anatomical findings for the five pamphiliid species examined.

TABLE I
Internal Anatomy Summary, Pamphiliidae

Species	C-L.C. or G.C.*	Malpighian Tubules	Salivary Glands
<i>Acantholyda</i> sp. 2		20 clumps, irregular	Bent duct, shorter gland
<i>Acantholyda</i> sp. 1	C-L.C.	15 clumps, regular	Bent duct, longer gland
<i>Cephalcia</i>	C-L.C.	11 clumps	Straight duct, longer gland
<i>Pamphilius</i>		7 clumps	Straight duct, shorter gland
<i>Neurotoma</i>	C-L.C., G.C.	7 clumps and wing formation	Bent duct, very short gland

*C-L.C. = Crypt-like cells.

G.C. = Gastric caeca.

Groupings of genera based on similarity of salivary glands do not agree with those based on hosts. However, more species should be examined to determine the validity of bent versus straight ducts as a "higher" character, grouping *Acantholyda* with *Neurotoma* on the one hand, and *Cephalcia* with *Pamphilius* on the other.

SUPERFAMILY TENTHREDINOIDEA

Family Pergidae

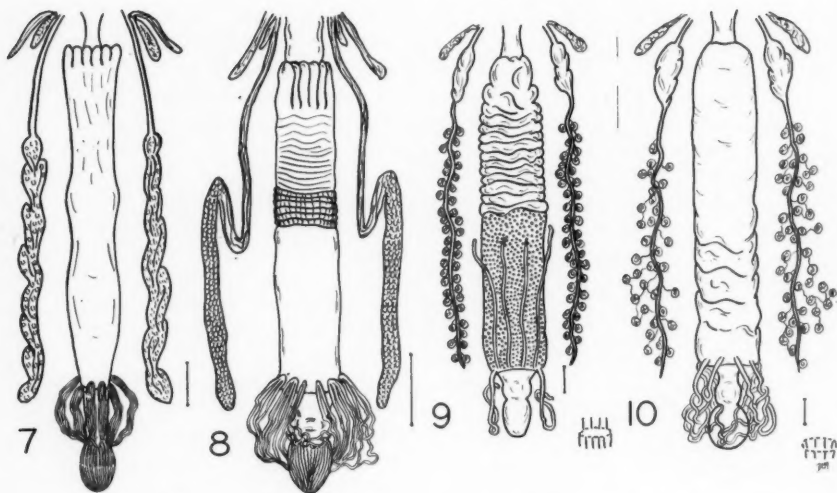
Subfamily Acordulecerinae

Acordulecera sp. Host, *Quercus alba* L. Location, Ottawa, Ont., Canada. Fig. 9, 139C.

A 1. Pharynx and oesophagus, slender, no trace of crop.

2. Two distinct regions to mid-gut; (1) heavily, transversely striate, deep folds over first half of gut, anterior third also cut by deep longitudinal folds; (2) extends smoothly to hind-gut, surface with somewhat "warty" appearance, broken at widely spaced intervals by single cell, crypt-like protuberances (cf. Cimbicidae).

3. Ordinary ileum, colon, and fairly large rectum.



Figs. 7. *Pamphilius* sp. 8. *Acantholyda* sp. 1. 9. *Acordulecera* sp. 10. *Acorduleceros megalcephalus* Benson.

- B. Ten evenly-spaced Malpighian tubules enter mid-gut separately: four on ventral surface directed anteriorly, floating freely in body cavity; two lateral and four dorsal directed posteriorly, bound loosely to rectum.
- C. Salivary glands, single pair, each duct with large anterior reservoir, narrowing posteriorly and coiling loosely. Gland cells attached individually by tiny secondary ducts, cells relatively few in number, large, up to ten times the main duct in diameter in the final instar (sketched as less). Emphasis on gland cell, not duct, in the *Acordulecerinae*.
- E. Sections of sucker-like, crescentic glands, lateral protuberances on abdominal segments 2-4 and 8, showing two cell types, large, globose cells interlaced by clumps of tall cylindrical, "ciliate" ones. Glands strikingly similar to sections of ventral abdominal non-eversible glands in some species of *Argidae*.

Acorduleceros megalcephalus Benson (Det. R.B.B.). Host, *Pisidium guajara*. Location, Brazil. Fig. 10.

- A 1. Pharynx and oesophagus, slender; no trace of crop.
- 2. Two distinct regions to mid-gut, first half smooth and straight, last half heavily transversely striate and thrown into deep folds.
- B. Eight evenly-spaced Malpighian tubules, directed posteriorly, loosely bound perirectally.
- C. Salivary glands, single pair with evidence of small accessory pair. Reservoirs, duct alignment, and large gland cells as in *Acordulecera*.

This species differs in two of the generally accepted characters from the *Acordulecerinae*. True crescentic, sucker-like protuberances are lacking, although a faint trace of crescentic sclerotization is visible in the areas occupied by glands in *Acordulecera* sp. The thoracic legs (5-segmented, distal segment with sharp claw and globose swelling, or empodium, in *Acordulecera*), in *Acorduleceros*

consist of five fleshy globular segments, without a definite empodium. A slight, fleshy suranal process is present in *Acorduleceros*.

The *Acordulecera* group has an interesting history. In 1906, MacGillivray (38) included the Acordulecerinae in his Tenthredinidae, and said the subfamily was monogeneric in North America. In 1911, Rohwer (47) included the subfamily in his Pterygophoridae, splitting it into the Acordulecerini (*Acordulecera*, *Pantherix*, and *Thulea*) and *Conocoxini* (*Conocoxa* and *Nithulea*). Konow (36) on the contrary, had considered *Acordulecera* one of 14 genera in his Lobocerotides (one of four tribes in his Lophyrini (=diprionid) group), although from his description it was fairly obvious that he had not examined any North American *Acordulecera* species in particular. In 1937, Ross (52) created the family Acorduleceridae, consisting of one genus, and pointed out some striking differences between this family and the Pterygophoridae. He stressed, at the same time, the close relationship of the two groups through their extremely similar male genitalia. Benson (4), in 1938, included the acordulecerids as one of the fourteen subfamilies of the family Pergidae, and there they have remained.

Although the generic name used by Benson is considered by Ross to be a synonym for *Acordulecera*, as used by Konow (36), *Acorduleceros megaloccephalus* is quite distinct from representatives of *Acordulecera* and Benson's terminology is followed here.

Subfamily Perginae

Perga dorsalis Leach. (Det. R.B.B.). Host, *Eucalyptus* sp. Location, Australia. Fig. 11.

- A 1. Pharynx, narrow; oesophagus and crop, broad; oesophageal diverticula present. The entire ventral body cavity is filled with a sac-like gland split into two lobular extensions. The gland itself resembles the pouches found in the Diprionidae. The latter, however, are oesophageal diverticula, whereas the *Perga* structure enters the pharynx almost in the region of the mouth opening. The sac fills the venter of the thorax, and is firmly attached to the body wall by means of fascia in the region of the second and third thoracic legs. The ends of the sac taper into fine ducts, which disappear mid-ventrally at the base of the coxae of the third thoracic legs. By manipulation of these sacs concentrated Eucalyptus juice could be ejected from both the mouth and the thoracic venter, presupposing somewhat the same function for these glands as for the oesophageal diverticula of the Diprionidae. Living larvae are necessary to check this point.
2. Smooth line of mid-gut broken slightly under one-third the distance to hind-gut by row of separate, yet contiguous, gastric caeca, somewhat maltese-cross-shaped. Posterior region of gut lightly, transversely striate.
3. Rectum large.
- B. From 30 to 36 Malpighian tubules enter the mid-gut separately, evenly-spaced, except for a slight mid-ventral gap. About eight tubules in all extend anteriorly, the rest posteriorly where they are lightly bound to the rectum. First two tubules on either side of mid-ventral line extend anteriorly, laterally, and finally posteriorly, elbowed in appearance.
- C. Salivary glands, single pair of main, traces of small pair of accessory. Broad main ducts extend to region of hind-gut bordered by two rows of gland cells, two to four cells entering by a common, minute duct. Salivary ducts in *Perga* are of the same broad expansible type as found in the Diprionidae.

F. Cuticle exceptionally thick with sclerotized plates in many places.

Cerealcus scutellatus W. F. Kirby. (Det. R.B.B.). Host, *Eucalyptus* sp. Location, Australia. Fig. 12.

- A 1. Pharynx and oesophagus, narrow; crop, huge, extending to first abdominal segment, at least as long as entire mid-gut. As in *Perga*, pharyngeal diverticulum enormous, attached to ventral body wall in region of second and third thoracic legs, with a small duct passing to the exterior at the base of each third coxa.
2. Mid-gut finely and deeply transversely striate over first and last third, smooth in middle. At slightly less than one-third the length a row of separate, contiguous, round, button-like gastric caeca present.
- B. Eighteen Malpighian tubules enter mid-gut separately. Six directed anteriorly on dorsal surface, 12 posteriorly on dorsal and ventral. Two Malpighian tubules meet at a 45° angle before a common entrance to the gut. Anterior tubules float freely in body cavity; posterior ones, loosely bound to rectum.
- C. Salivary glands, as in *Perga*, similar to large expansible glands of the Diprionidae. Approximately two rows of gland cells empty into duct from two to four per cluster.

Benson (4, 5) stresses such primitive characters of the Perginae, as the retention of preapical tibial spines, but adds that far too little is known of the larvae for generalizations to be made. The absence of abdominal pseudopods in the free-living Perginae is, to him, one of the "remarkable cases of specialization" to be found in sawflies. In his revision of the genus *Perga*, Benson (5) subdivides the subfamily into two tribes and eight genera.

Subfamily Pterygophorinae

Lophyrotoma cyanea Leach. (Det. R.B.B.). Host, *Eucalyptus* sp. Location, Australia. Fig. 13.

- A 1. Pharynx, narrow, oesophagus or crop, squat or bulbous. No pharyngeal diverticulum.
2. Deep longitudinal folds and transverse sculptoring for a distance slightly under one-third the length of the gut; remainder smooth. Row of separate, rectangular, fluted gastric caeca, strikingly similar to those to be seen in the Argidae, mark transition between striate and smooth portions.
- B. Approximately 42 Malpighian tubules enter mid-gut separately at evenly spaced intervals. Each tubule extends approximately one-ninth or one-tenth the length of mid-gut anteriorly, coils loosely posteriorly where lightly bound perirectally.
- C. Salivary glands, only one pair of main apparent but small pair of accessories may have been overlooked. Each main duct enters large, anterior reservoir thickly coated by small glandular cells, extends posteriorly as a slender duct sending off numerous side branches of smaller diameter. Branch ducts, in turn, rimmed by rows of separate gland cells, each cell with an individual attachment. The general salivary gland appearance that of the grape-like gland-cell arrangement of the Argidae.
- F. Cuticle thin, stiffened by heavily sclerotized, cone-like warts, 3 rows per segment. Glandubae on subspiracular lobes. *Lophyrotoma* larva,

armoured and stream-lined in appearance, possesses a long slender tail, one-quarter the length of the entire body.

Benson (3, 4) shows that the Pterygophorinae possess few of the main characteristics of the subfamilies of the Pergidae complex. Unless the characters are invalid as fundamental indices, this would tend to indicate a relatively specialized subfamily.

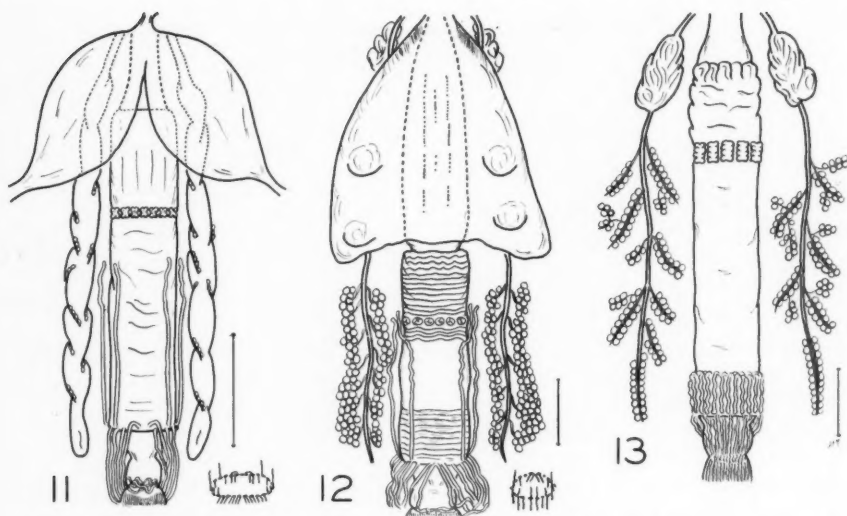
According to Benson (4) it is safer to consider the Pergidae as a single family of 14 subfamilies, than to upset the balance of the whole group by giving family status to some. He is of the opinion that, if current theories of a many-veined Hymenopterous wing being ancestral and xyelid-like are correct, the Pergidae, with extreme reduction in venation and modification of other characters, are at the specialized end of the scale.

It has long been recognized that the pergid complex was close to the Argidae, Diprionidae, and Cimbicidae. Larval morphology provides evidence that it is a group possessing characters hitherto considered to be the attributes of other families, e.g. the empodium of Argidae and the winged spiracles of Cimbicidae. Their internal anatomy reveals even more striking character associations (see Table 2).

Examination of five species in three subfamilies of a subfamily complex is obviously not conclusive; it is hoped, however, that Table 2 may stimulate interest in the possibility that larval characters will help to clarify the pergid complex. Comparing the three Pergidae subfamilies, the Argidae, Cimbicidae, and Diprionidae, it would be reasonable to recognize a salivary trend from the

TABLE II
Internal Anatomy Summary, Argidae, Pergidae, Diprionidae, Cimbicidae

Group	Salivary Type	Malpighian Type	Diverticulum	Gastric Caeca
Argidae	argid	specialized argid		argid
Pergidae				
Pterygophorinae				
Lophyrotoma	argid-like	42, diprionid-like		argid-like
Acordulecerinae				
Acordulecera	argid-like	10, xyelid-like		crypt cells
Acorduleceros	argid-like	8, xyelid-like		
Perginae				
Perga	diprionid-like	30-36, diprionid-like advanced	pharyngeal	maltese-cross shaped
Cerealces	diprionid-like	18, diprionid-like advanced	pharyngeal	button-shaped
Diprionidae	diprionid	diprionid	oesophageal	crypt cells
Cimbicidae	diprionid-like	specialized, closest to argid-like		crypt cells (indicating caeca or gastric diverticulum in <i>Cimbex</i>)



Figs. 11. *Perga dorsalis* Leach. 12. *Cerealces scutellata* W. F. Kirby. 13. *Lophyrotoma cyanea* Leach.

grape-like Argidae arrangements through the argid-like Pterygophorinae (gastric caeca of these almost identical) and the Acordulecerinae, to the Perginae with its diprionid salivaries (and pronounced gastric caeca), the Cimbicidae, and, finally, the Diprionidae; or, in view of the diverticula, to the Diprionidae and, finally, the Cimbicidae. As far as degree of specialization in the Malpighian tubules is concerned, the spacing and number of *Perga* tubules is a slight advance on the average stage reached in the Diprionidae examined, (e.g. *Neodiprion*), whereas, in the reduction in number and mid-ventral fusion of tubules, *Cerealces* is more specialized than *Perga*. *Lophyrotoma* is theoretically at the level between the Diprionidae examined and *Perga*; the two species in the Acordulecerinae have the primitive xyelid-like arrangement and thus represent the lowest level in this group. The Argidae and the Cimbicidae, as will be demonstrated, represent the most specialized level.

Family Argidae

Subfamily Arginae

Arge pectoralis (Leach). Host, *Betula papyrifera* Marsh. Location, Ottawa, Ont., Canada. Figs. 14, 138, 139A.

- A 1. Pharynx and oesophagus, narrow; no crop. Well-developed oesophageal invagination projects into mid-gut lumen, middle flaps of clear ovoid cells.
2. Mid-gut, two main regions: (1) slightly over one-third the length of gut marked by four, deep longitudinal folds and prominent transverse striations, delimited posteriorly by a complete ring of gastric caeca evenly distributed, each caecum with long and short lobe-like projections; (2) extends to hind-gut, divided into three or four fairly constant subdivisions by muscular constrictions; mid-ventral line of mid-gut marked by slightly protruding typhlosole-like ridge, tubules entering gut at junction with hind-gut.

Epithelial cells in (1) thrown into constant series of ridges suggestive of regenerative crypts; however, ridges do not project through muscle layers and are not co-ordinated with the transverse striations already noted. Cells, tall and slender, occasional cell goblet-shaped. In (2) posterior to caeca, rectangular epithelial cells give way to taller epithelium near hind-gut junction. Peritrophic membrane extends from region of oesophageal invagination to gastric caeca as single-layered sac. Corresponding with the change from rectangular cells to a taller epithelium in (2), the membrane appears as a two-layered structure, giving way to a sharply defined series of four or five layers, indicative of increased membrane formation in the posterior part of (2).

3. Colon, short bulb-like; rectum, fairly large.
- B. Two common stalks of Malpighian tubules enter typhlosole region on mid-ventral line separately through crescentic opening. Main axes of stalks at 45° angle anteriorly with longitudinal axis also directed slightly dorsally. Each stalk branches into approximately 19 tubules, all directed posteriorly and, finally, firmly bound to rectum.
- C. Salivary glands, three pairs of main, and pair of small accessories. Innermost ducts slightly smaller in diameter than two similar outer pairs. Gland cells of inner ducts extremely large, from five to ten times diameter of duct, individually attached. Cells of outer ducts slightly over one-half the diameter of inner cells, grape-like clusters of two or three opening into smaller ducts. The size difference and other correlated histological differences, which make separation of the cells possible, could be the result of irregular timing of secretion; however, the single duct attachment, as opposed to a grape-like arrangement, appears to be a real difference. Anterior region of outer salivary ducts with reservoir enlargements, as in *Acordulecerinae*. Lumen of reservoir in *Argidae* not so wide as that of *Xyelidae*, more a thick accumulation of smaller, tightly-packed cells around a slight enlargement of the duct.
- D. Fat body, thick; fat cells smaller peripherally, larger in main body sheath; three main divisions to body sheath; surrounding gut, binding tubules, and covering rectum.
- E. Seven ventral-abdominal, non-eversible glands located just beneath ventral nerve cord, each gland directly under, but separate from, a nerve ganglion. Minute ducts ventrally from glands to exterior, opening between abdominal prolegs of segments 1 to 7 and the mid-venter. Final gland smaller. Each gland consists of a lumen filled with "secretion products", lined by large, darkly haematoxylin-staining irregularly rounded cells and clumps of taller, cylindrical cells, similar to the crescentic gland structure in *Acordulecera*. Glandular structure situated on mid-ventral line between pro- and meso-thorax. Many epidermal glands seen in sections.
- F. Three-layered cuticle thick and patterned. Either extremely thick epicuticle present or, as in the *Pamphiliidae*, secretion from the epidermal glands laid down over epicuticle contributing to a scaled or ridged appearance. Occasional spines found deeply embedded in cuticle.

Larvae feeding on *Alnus* and separable from *Arge pectoralis* in their possession of black epiprocts (as opposed to the orange of *pectoralis*), and of more

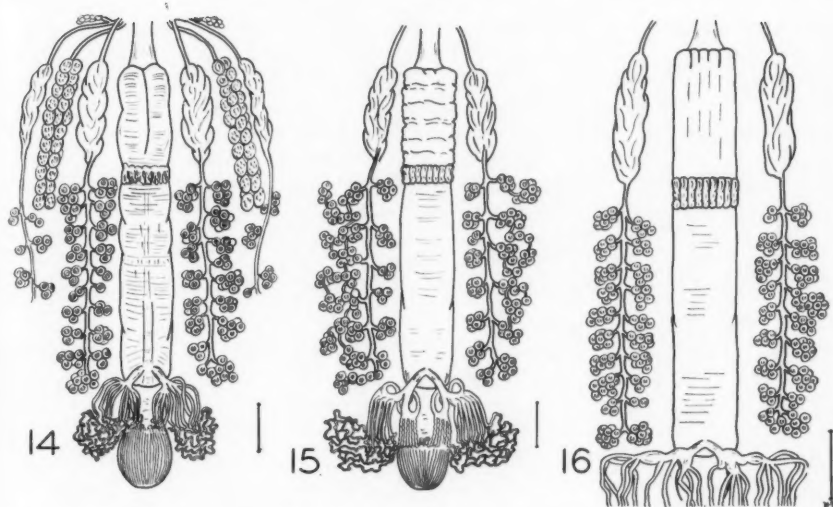
distinct body markings, are generally identified as *Arge clavicornis* (Fab.) (a term implying an entire complex of forms, Ross, 53). They are, however, similar in internal anatomical detail, except for minor differences in number and shape of gastric caeca. Additional specimens with similar anatomy, which are easily separable from *pectoralis* on external larval characters (see Table 3), are an *Arge* sp. not *clavicornis* found on *Alnus*, an *Arge* not *pectoralis* on *Betula*, and an *Arge* on *Crataegus*. The external differences noted in certain cases are much more extreme than one finds within a population of larvae; intermediates are not apparent.

Arge annulipes Klug. (Det. R.B.B.). Host, *Rumex sagittatus*. Location, Grahamstown, South Africa. Fig. 15.

- A. 1. Similar to fore-gut of *A. pectoralis*.
2. Mid-gut, first one-third delimited posteriorly by ring of gastric caeca, is marked by approximately seven deep, transverse folds. Gastric caeca longer than those of *pectoralis*, same number, 12, present, remainder of gut smooth.
- B. Two common stalks of Malpighian tubules fuse before entering mid-venter of mid-gut. Main axes of stalks at 45° angle with each other, each extends posteriorly and branches (at about twice the distance from the gut origin that branching begins in *pectoralis*). Each stalk divides into two main branches, one extending latero-dorsally around the gut somewhat as in the wing-like extension in *Neurotoma* and sending off seven parallel branches which are collected and bound rectally. The other branch, extending directly posteriorly, sends off five tubules oddly waved in appearance resulting from the wide diameter of tubule and alternating permanent bulbs along length. These also are bound perirectally.
- C. Salivary glands, single set of main. Similar ducts and grape-like branching of gland cells as in outer glands of *pectoralis*. Grape-like branching more complicated than in *pectoralis*, with indication of secondary branching between adjacent clusters. Similar reservoir regions at anterior end of each duct.
- E. No trace of ventral-abdominal non-eversible glands.

Arge micheli du Buysson. (Det. R.B.B.). Host, *Rumex nervosus* Vahl. Location, Adi Ugri, Eritrea. Fig. 16.

- A 1. Fore-gut as in preceding species.
2. Mid-gut narrowly longitudinally striate for almost first one-third the length, to ring of tall, wasp-waisted gastric caeca; remainder lightly transversely striate.
- B. Two common stalks of Malpighian tubules join before entering mid-gut. Each stalk extends laterally from point of entrance in two smooth humps to loose branching of approximately eight tubules per side (some evidence of secondary branching). Tubules extend posteriorly, bound perirectally.
- C. Salivary glands, single set of main as in *Arge annulipes*, but no secondary duct-branching.
- E. No ventral-abdominal non-eversible glands.
- H. Although the large *Arge micheli* larva is quite distinct from *Arge ochropus*, the adult *micheli* keys to "close to *ochropus*" in Benson (7).



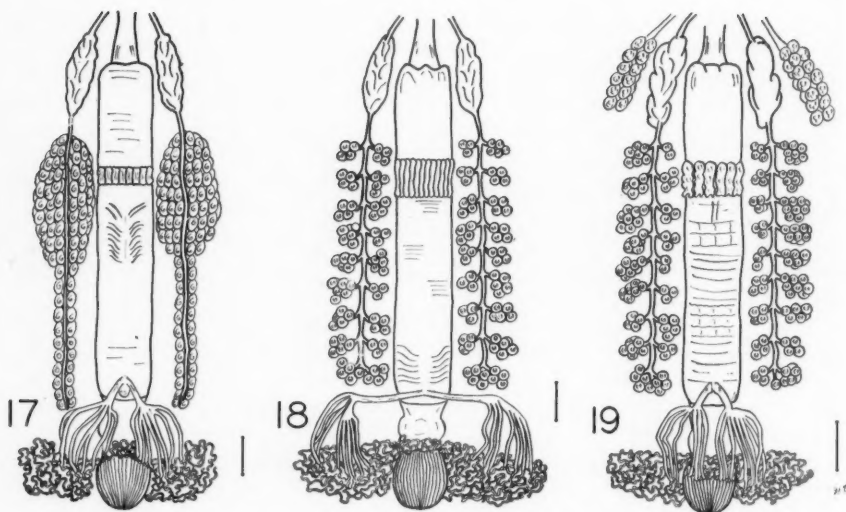
Figs. 14. *Arge pectoralis* (Leach). 15. *Arge annulipes* Klug. 16. *Arge micheli* du Buysson.

Arge ochropus (Gmelin). (Det. R.B.B.). Host, *Rosa* sp. Location, England. Fig. 17.

- A 2. Mid-gut fairly smooth to ring of gastric caeca approximately first one-third, remainder of gut deeply transversely striate; typhlosole-like fold on mid-ventral line.
- B. Typhlosole widens into oval sac on mid-ventral line at junction of mid- and hind-gut. Two common tubule stalks enter this sac at a 60° angle; extending posteriorly, each stalk branches at about the level of the colon, into approximately eight Malpighian tubules, collected and bound perirectally.
- C. Salivary glands, one pair of main, anterior reservoir, ducts bordered by single cell layer of extremely large, pear-shaped cells individually attached. Appearance and structure that of the innermost gland pair in *A. pectoralis*.

Arge sugilloides Pasteels. (Det. R.B.B.). Host, *Royena* (Ebenaceae). Location, Grahams-town, South Africa. Fig. 18.

- A 2. Mid-gut lightly, longitudinally lobed about first one-third of length to ring of gastric caeca. Caeca very long, slender, approximately 4-lobed each end, fluted down length. Remainder of gut loosely, transversely striate, with prominent typhlosole-like structure.
- B. Two common stalks of Malpighian tubules fusing just before entrance to typhlosole region; axes of stalks at right angles to mid-ventral line. Stalks extend laterally as long, whiskery branches until each divides into two main branches, and these in turn into approximately four. Tubules collected perirectally. Division of stalks begins about three times as far laterally as in *pectoralis*.
- C. Salivary glands, one set of main. Grape-like branching arrangement of salivary gland cells and secondary branching lacking, as in *Arge micheli*. Reservoirs anteriorly.



Figs. 17. *Arge ochropus* (Gmelin). 18. *Arge sugilloides* Pasteels. 19. *Arge* sp. 1.

Arge sp. 1. Host, *Salix* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 19.

- A 2. Mid-gut lightly, longitudinally lobed to region of tall, loosely lobular gastric caeca. Deeply transversely striate to end of gut, typhlosole-like structure prominent.
- B. Two common stalks of tubules enter mid-gut separately, almost touching at base of typhlosole, forming roughly 60° angle as in *ochropus*. Each stalk extends some distance posteriorly before branching into approximately eight tubules collected and bound perirectally. Strikingly similar in arrangement to *A. ochropus*.
- C. Salivary glands, one set of main. Grape-like branching arrangement, no secondary branching. Reservoirs anteriorly.

Taxonomically keys to, or close to, *Arge enodis* L. a *Salix* feeder in England.

Subfamily Atomacerinae

Atomacera sp. (Det. R.B.B.). Host, *Brasso ipomoea*. Location, Trinidad. Figs. 20, 139B.

- A 1. Pharynx and oesophagus, narrow; no crop.
- 2. Mid-gut with longitudinal folds to ring of gastric caeca approximately one-third the length. Caeca, approximately same size as those of *pectoralis*, so close together as to be almost fused into a raised band above the gut. Remainder of gut lightly, transversely striate.
- B. Common Malpighian tubule stalk extends anteriorly from entrance to mid-gut. Stalk divides into two, each branch curving posteriorly, and splitting into two about level of junction of mid- and hind-gut. These divide in turn, each sending two to five tubules posteriorly to be bound perirectally.
- C. Salivary glands, single set of main. As in *ochropus*, gland cell arrangement that of innermost *pectoralis* glands. Cells larger than those of

ochropus, reservoir region only faintly delimited, more an accumulation of smaller gland cells about anterior end of duct.

- E. Larva externally noteworthy for possession of single row of tall, transparent glands, milk-bottle in shape. Each gland consists of a core, a modified epidermal cell or cells, and a tall, cuticular, flexible, protruding sheath with a distal thickening and an opening to the exterior. Entire effect that of a "ciliate" or plush-covered larva.

Subfamily Sterictiphorinae

Sterictiphora sp. (Det. H.H.R.). Host, Unknown. Location, Illinois, United States. Fig. 21.

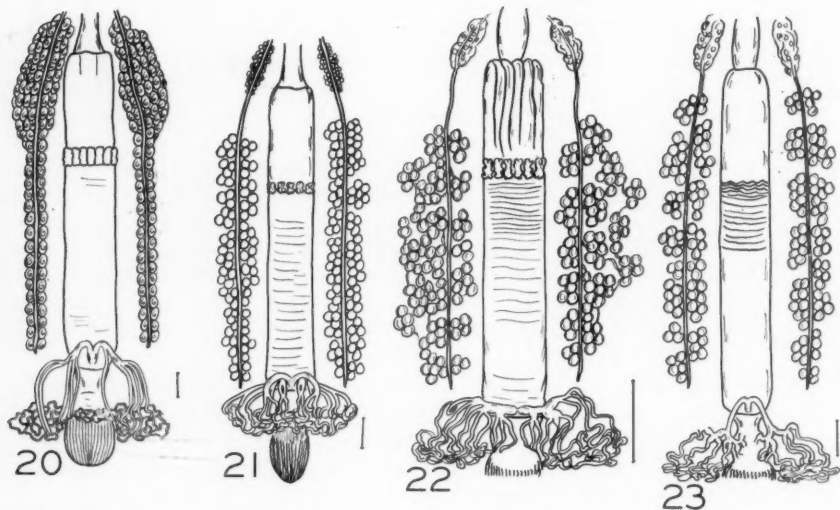
- A 1. Pharynx narrow; oesophagus enlarged into slight crop.
2. Mid-gut extends smoothly for first third length to ring of faint yet distinct gastric caeca. Remainder deeply transversely striate. No typhlosole.
- B. Malpighian tubules, single short common stalk enters gut, branches anteriorly and laterally into two widely curving secondary stalks. Each stalk swings posteriorly, ends in two posteriorly directed tubules. At widest portion of curve, each stalk gives off a wide Malpighian tubule branch which splits immediately into two, and a second branch which splits into two farther posteriorly. On outermost part of curve, common lateral stalk is given off which also divides into two. Very similar to *Atomacera* sp.
- C. Salivary glands, single pair of main, accumulation of small gland cells anteriorly. Slender ducts thickly coated with large gland cells, short, grape-like branching as in inner pair of *Sofus*.
- E. Milk-bottle glands protruding, single one on latus of each second annulet. Similar to glands of *Atomacera* sp.

Schizocera krugii Cresson. (Det. H.H.R.). Host, Unknown. Location, Puerto Rico.

Presumably *Sterictiphora krugii* Cresson of Peterson. Puerto Rican Sawfly on *Coccolobis uvifera*, (sea-grape). Fig. 22.

- A 1. Pharynx, narrow; oesophagus enlarging into slight crop.
2. Mid-gut deeply longitudinally striate one-third the length to ring of large, prominent gastric caeca. Remainder of gut deeply transversely striate. No trace of a typhlosole.
- B. Malpighian tubules, two common stalks fuse just before entrance to gut, narrow, strap-like fusion. The broad oval stalks are at right angles to the mid-ventral line. Each stalk extends laterally giving rise to two main posteriorly extending branches each dividing into three tubules, continues partially encircling gut ending finally in a third branch splitting into three tubules. The heads of the main branch stalks are swollen. All tubules bound posteriorly. Malpighian arrangement strikingly similar to that of *Arge micheli*.
- C. Salivary glands, single set of main. Large salivary-gland cells, grape-like clustering in two rows, similarity greater between *krugii* salivary and the grape-like set of the Arginae, than the former and the two *Sphacophilus* spp. or *Sofus*.
- E. Fairly large, transparent rounded protuberances capped by a slight nipple-shaped extension, mark the surface of *krugii* and the two species of *Sphacophilus* examined.

In *Schizocera krugii* and the two species of *Sphacophilus*, larvapods are prominent on abdominal segments 2 to 7 and 10, and present in slightly reduced but definite form on 8, and in *cellularis*, on 9. *S. krugii* and *Sphacophilus* have clear sac-like protuberances one on each ventral side of the subspiracular lobe of each abdominal segment, "pontoon-like" in effect. These two species have, in addition, sac-like protuberances one on each side of a larvapod with the result that in ventral view there seem to be two sets of larvapods present.



Figs. 20. *Atomacera* sp. 21. *Sterictiphora* sp. 22. *Sterictiphora krugii* Cresson. 23. *Sphacophilus cellularis* (Say).

Subfamily Sericocerinae

Sphacophilus cellularis (Say). (Det. H.H.R.). Host, *Convolvulus sepium* L. Location, Illinois, United States. Fig. 23.

- A 1. Pharynx, narrow, oesophagus enlarging into slight crop.
- 2. Mid-gut smooth for one-third the length, followed by slightly transversely ridged portion for approximately one-fifth the length. Remainder smooth.
- B. Malpighian tubules, common stalk extends anteriorly from mid-gut entrance. Stalk divides, each branch curves posteriorly, and redivides in region of colon. These tubules divide in turn, outermost into three branches innermost into three with one redividing, all directed posteriorly, bound perirectally. The tubules differ widely in diameter from the colon region on, suggesting specialization in the form of alternating tubule bulbs and narrow connections. The Malpighian arrangement in *cellularis* is similar to that of *Atomacera* in type of fusion at the mid-ventral line.
- C. Salivary glands, single set of main. Salivary-gland cells large, round, grape-like arrangement with cell clusters more closely associated with

the ducts than other species in the Arginae. Similar to innermost set of glands in *Sofus*. Reservoir region faintly delimited, an accumulation of smaller gland cells about anterior end of duct. Single layer effect differs from that of *Atomacera*.

Sphacophilus plumiger (Klug). (Det. H.H.R.). Host, *Apios tuberosa* Moench. Location, Illinois, United States. Fig. 24.

- A 1. Pharynx, narrow; oesophagus enlarging into a slight crop.
- 2. Mid-gut lightly longitudinally striate anteriorly, fairly smooth to ring of gastric caeca about one-third the distance along mid-gut. Smooth posteriorly until last twelfth of gut marked by deep transverse striations and a typhlosome-like fold.
- B. Malpighian tubules, single common stalk, rectangular in shape, at right angles to mid-venter at entrance. Posteriorly extending stalks constricted off laterally. Each branch stalk swings about gut sending off two posteriorly directed stalks on each side the mid-line (each dividing in turn into two), and three single posteriorly extending tubules, bound perirectally. Malpighian arrangement close to *Arge ochropus* and *A. micheli* in tubules, to *Atomacera* in fusion type and *Sphacophilus cellularis*.
- C. Salivary glands, single set of main. Large, round salivary-gland cells, grape-like arrangement, with clusters closely associated with ducts as in *cellularis*.

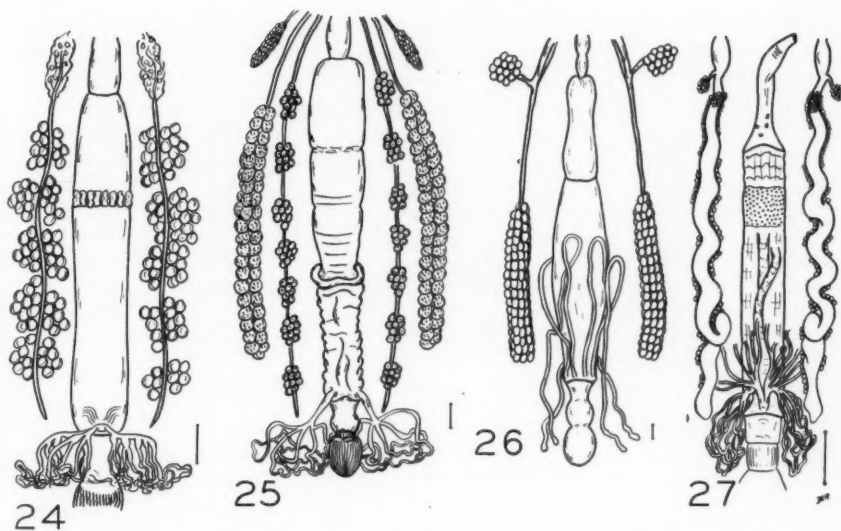
Sofus pilicornis (Holmgren). Host, *Portulaca*. Location, Sault Ste. Marie, Ont., Canada. Fig. 25.

- A 1. Pharynx, narrow, oesophagus enlarging into slight crop.
- 2. Mid-gut, two regions: (1) slightly over one-half of mid-gut in length, generally smooth, constricted into three bulbous portions by tight muscular bands. First band somewhat raised, only not in the proportions of gastric caeca, no crypt cells; (2) extends to hind-gut, deeply convoluted, both transversely and longitudinally, extends over region (1) in a deep fold rimmed by a fleshy ring. Net result is a telescoping of the end of region (1) into region (2).
- B. Two common stalks of Malpighian tubules enter mid-gut on lateral surface, slightly ventral of a mid-lateral line. Main axis of stalk forms a 45° angle with mid-ventral line. Stalk extends some distance posteriorly, branches into five tubules, which continue to rectum and are tightly bound.
- C. Salivary glands, two sets of main, single set of accessory. Innermost glands with branching, grape-like arrangement, outer with large, individually-attached gland cell arrangement. Grape-like cell clusters more closely attached to their ducts than in other species examined in the Argidae.
- E. Prominent, sclerotized, conical projections, single row per segment present, presumed glandular in nature.

At the present time any North American sawfly larva with a typically flattened "argid" appearance and splayed out thoracic legs is apt to be classified as *Arge pectoralis*, or, if the larva with a dark epiproct were found feeding on alder, as *Arge clavicornis*. The adult taxonomy of North American forms is

TABLE III
External Larval Characters, Argidae

Species and Host	Abdominal Segments with larvapods	Antennae	Ventral-Abdominal glands	Colour of Epiproct	Head	Body
<i>Arge pectoralis</i> (Birch)	2-6, 10	2 segments, "cone"	7 (7th small)	yellow-orange	orange	spotted
<i>Arge clavicornis</i> (Alder)	2-6, 10	"	"	black	orange	spotted-striped
<i>Arge</i> sp. (Alder)	2-7, 10 (rudimentary, 8)	low-mound mosaic "button-like"	7	yellow (spotted)	orange marked clypeus epicranial line dark	pale, lightly spotted
<i>Arge</i> sp. (Hawthorn)	2-6, 10	high-mound mosaic = "cone"	7	black	black, clear clypeus	shiny, blue-black lines darker than <i>clavicornis</i>
<i>Arge</i> sp. (Birch)	2-6, 10	2 segments, "cone"	7	yellow	black	pale, lightly spotted
<i>Arge annulipes</i> (<i>Rumex</i>)	2-6, 10 (rudimentary 7, 8)	intermediate-mound mosaic "button-like"	1 (on seg. 8)	yellow	orange, marked dark clypeus side eyes	pale faint spots
<i>Arge micheli</i>	2-6, 10 (rudimentary 7, 8, 9)	high-mound mosaic = "cone"		yellow	orange	shiny blue-black spots
<i>Arge ochropus</i> (<i>Rosa</i>)	2-7, 10 (rudimentary 8, 9)	low-mound mosaic "button-like"		yellow	orange	pale
<i>Arge sugilloides</i> (<i>Royena</i>)	2-5, 10 (rudimentary 6, 7, 8)	high-mound mosaic = "cone"		black	black clear clypeus	pale, shiny brown spots hirsute
<i>Arg.</i> sp. 1 (Willow)	2-7, 10	low-mound mosaic "button-like"	7	yellow	dark and light heads	yellow, finely spotted
<i>Atomacera</i> sp. (<i>Brasso</i>)	4-8, 10	high-mound mosaic = "cone"				"milk-bottle" glands
<i>Sterictiphora</i> sp.	2-7, 10	high-mound mosaic; round 2-segmented cone			orange	"milk-bottle" glands
<i>Schizocera klugii</i> (<i>Coccolobis</i>)	2-7, 10 1, 8, trace	low-mound mosaic			orange, brown	swollen gland mound
<i>Sphacophilus cellularis</i> (<i>Convolvulus</i>)	2-9, 10 1, trace	flat, low mound			eye patches clypeus orange	swollen gland mound
<i>Sphacophilus plumiger</i> (<i>Apios</i>)	2-7, 10 1, 8, trace	low-mound			orange	swollen gland mound
<i>Sofus pilicornis</i> (<i>Portulaca</i>)	2-8, 10	low-mound mosaic "button-like"			mottled	



Figs. 24. *Sphacophilus plumiger* (Klug). 25. *Sofus pilicornis* (Holmgren). 26. *Blasticotoma filiceti* Klug. 27. *Zaraea* sp.

likewise unsettled and no attempt has been made so far to compare such forms with the fairly well-established species of the British Isles and Continental Europe. Current knowledge of *Arge* distribution, renders it likely that many holarctic species exist but are simply unrecorded in North America at present. Additional information on tropical forms (see Benson (4) for at least eight additional sub-families) is required before the extent of variation in the Argidae will be known and understood.

It is interesting that Ross (52) mentions that one of his primitive characters, the possession of pre-apical spurs, is typical of the Arginae alone in the Argidae. This seems to indicate, as do other larval and adult characters, that *Arge* is more primitive than *Atomacera* and *Sofus*.

Yuasa (69) made perhaps the first thorough separation of the larvae in the genus *Arge*. He claimed species were divisible into two sections by the structure of the antennae and the number of larvapods, and used these characters in a key, which served the purpose for his own collection and now seem of fundamental importance for additional species. His antennal characters were "conical or peg-like" as opposed to "button-like". Table 3 makes use of Yuasa's characters as well as additional, generally descriptive ones.

Yuasa (69) associates the presence of conical antennae with the presence of larvapods on abdominal segments 2-6 and 10 (rudimentary on 7) and button-like antennae with larvapods on 2-7 and 10 (rudimentary on 8). As seen in Table 3, the apparently 2-segmented "cone" effect is found on larvae with larvapods on 2-6 and 10 (also described as "high-mound mosaic" in cases where the cone is a wider, subdivided extension), on *Arge sugilloides* with larvapods on 2-5 and 10 (rudimentary on 6, 7 and 8), and in *Atomacera* sp., with larvapods on 4-8 and 10. "Button-like" or "low-mound mosaic" is found, as Yuasa's results would

indicate, on larvae with larvapods on 2-7 and 10, in *Sofus* with larvapods on 2-8 and 10, and in *Schizocera* and the two species of *Sphacophilus*. *Sterictiphora* sp. is an exception.

Ross (52) visualizes the Tenthredinoidea as branching off from other forms before the primitive sawfly pattern had changed greatly. The earliest groups to emerge, he believes, were the Pergidae, Argidae, Lobocoridae, Perreyiidae, and the pterygophorid-acordulecerid complex. Yuasa, following MacGillivray's lead, placed his Hylotominae (=argid group) between the Blennocampinae and Fenusinae, stressing a resemblance to the Schizocerinae and Acordulecerinae among his more specialized subfamilies in the Tenthredinidae. He was not unaware of such larval characteristics as 6-segmented thoracic legs and extreme variability in number of larvapods (from five to nine pairs plus one rudimentary pair), seemingly indicative of a nearer approach to the xyelid larva, with its full larvaped complement.

As shown incidentally in table 2, the Pterygophorinae and Acordulecerinae (the latter included in the Pergidae), possess argid-like salivary glands, a striking corroboration of their close relationship when the internal anatomy of all the species studied is taken into consideration. The emphasis upon increased branching of narrow ducts and numbers of salivary glands arranged in clusters might be considered indicative of a trend from small ducts and large gland cells, in the Xyelidae, to huge ducts with rows of small gland cells, in the Diprionidae, Cimbicidae, and Tenthredinidae.

Within the Argidae, the genera examined seem to be at a relatively advanced level, as found in the species described in the Cimbicidae and some Tenthredinidae. Malpighian tubule arrangements are simple variations of the same basic plan. Although it is tempting to arrange the species of *Arge* on the basis of the relative length of the main stalk before branching begins, or the direction of the stalks, no more may be said with certainty than that *A. pectoralis* and similar species resemble most closely the *Sofus* Malpighian arrangement, that *Arge annulipes* and *A. sugiloides* are closer to *A. micheli* and that *Arge* sp. 1, *Arge ochropus*, and *Atomacera* sp. are fairly similar. If one accepts the two types of salivary arrangements apparent in *A. pectoralis*, one might postulate the following groupings: (a) the retention of both types in *Sofus*; (b) modification of argid grape-like arrangement in *Sphacophilus plumiger*, *S. cellularis*, and *Sterictiphora* sp., (c) the true grape-like arrangement in *Arge annulipes*, *Arge micheli*, *Arge sugiloides*, *Arge* sp. 1, and *Schizocera*; (d) the large gland cell single-attachment arrangement in *Atomacera* and *Arge ochropus*.

Ventral-abdominal non-eversible glands are evidently not typical of the Argidae as a whole, and the significance of gastric caeca, important in the Arginae and probably in the Atomacerinae, cannot be evaluated until further species have been studied.

Family Blasticotomidae

Blasticotoma filiceti Klug. (Det. R.B.B.). Host, Filicales. Location, England. Fig. 26.

- A
1. Pharynx, slender; oesophagus, pear-shaped; crop about two-thirds the length of mid-gut.
 2. Mid-gut short, slender, pear-shaped tube.
 3. Hind-gut unmodified.
- B.
- Four Malpighian tubules enter mid-gut ventrally and ventro-laterally. Each extends anteriorly about two-thirds the gut-length, coils loosely,

posteriorly, tightly bound perirectally. Three parts to each tubule: narrow anterior part widening gradually to turn posteriorly; broad, fairly flat posterior region; very narrow in diameter in rectal region.

- C. Salivary glands, one pair of main, small set of accessory, off former posterior to reservoir-like anterior enlargement of main ducts. Main duct continues as narrow, straight tube posteriorly to reservoir, surrounded by large round (globular) gland cells opening individually into the duct. Cells are over six times duct in diameter and surround it in a compact mass of approximately four cells at any one level. General appearance that of a xyelid gland except for shape of cells and somewhat looped effect in the Xyelidae.

Yuasa (69) wrote that the Blasticotomidae contained a single, monospecific genus confined to central and western Europe, an archaic type: "the systematic position of this unique species has been considered differently by practically every writer who has studied it. MacGillivray (1906) has shown, however, that it is, in certain of its characters, closely allied to the Xyelidae and Pamphiliidae, while in others it approximates the Tenthredinidae, and that it is intermediate in position between these two groups." Unfortunately, there were no literature references available to him of the immature stage of the Blasticotomidae, let alone material, and he was unable to check MacGillivray's hypothesis. Benson (4) mentioned the distribution of the Blasticotomidae (Palearctic and Oriental regions), that there were three species in two genera (*Blasticotoma* Klug and *Runaria* Malaise) and that the larvae were fern stem-borers lacking abdominal legs. Adult descriptions suggest a similarity of the Blasticotomidae, the Argidae, and Cimbicidae (4, 7).

Anatomical details in the *Blasticotoma* larvae are interesting in view of these suggested relationships. The salivary glands are closer in structural detail to the Xyelidae than to any other sawfly group, which places the two families very close together. It is interesting that 7-segmented larval "antennae" are found in three sawfly families, Xyelidae, Blasticotomidae, and Pamphiliidae. The salivary glands, with individual attachment to the ducts in the Argidae, are of the same general type as those of *Blasticotoma*, suggesting the same line of development. The loss of larvapods and the retention of subanal and other appendages on the final abdominal segments suggest that *Blasticotoma* is closest to the Pamphiliidae; however, the fact that the male genitalia are strophandrious suggests that the relationship is, on the contrary, with the line of strophandrious development leading from the Xyelidae to the Tenthredinoidea and implies a loss of larvapods occurring in the Strophandria as well as the Orthandria (see also the Xyelinae). The low Malpighian tubule number, four, in *Blasticotoma*, and the specialized nature of the tubules, added to absence of preapical tibial spines in the adult, unique wing venation, and the boring habit of the species, suggest that *Blasticotoma filiceti* is a rather advanced form within its own group.

Family Cimbicidae

Zaraea probably *inflata* Norton. Host, *Lonicera*. Location, Ottawa, Ont., Canada. Fig. 27.

- A 1. Pharynx, narrow, oesophagus, long, cylindrical, pear-shaped, approximately twice length found in other species of Cimbicidae, extends in stalk formation to junction with mid-gut. Region expansible into crop. Surface of fore-gut marked by occasional protruding tubercle, more the appearance of a glandular excrescence than of a crypt-like protuberance.

2. Mid-gut, three regions: (1), one-sixth of gut length, longitudinally and transversely striated muscular portion roughly corresponding to region in *Cimbex* and *Trichiosoma*; (2), one-sixth length of mid-gut with crypt-like protuberances scattered about surface, roughly comparable to regions 2 and 3 in *Cimbex* and *Trichiosoma*; (3), pronounced longitudinal folds and transverse striations present, typhlosole-like ridge along gut. Mid-gut proportionately reduced in *Zaraea* relative to *Cimbex* and *Trichiosoma*.
- B. Malpighian tubules, single large common stalk entering mid-ventral region, extending anteriorly, dividing into two branches, in turn giving rise to five tubules extending anteriorly and one or two tubules each extending posteriorly. Some secondary tubule-branching but less than in *Trichiosoma*. The tubule arrangement in *Zaraea* could have resulted from a fusion of the two *Trichiosoma* stalks for some distance from the entrance to the gut and a subsequent reduction in overall tubule number.
- C. Salivary glands, single pair of main, small pair of accessory. Main ducts large, expansible, coiled tubes extending length of body. Slightly bulbous reservoir present anteriorly, accessory off distally. Gland cells smaller than cluster cells of *Arge*, about one-quarter to one-eighth diameter of salivary duct when expanded. Individual attachment of cells to duct, two single rows of cells along length of duct, indication of clumping of cells before joining anteriorly. General appearance diprionid-like.

Abia sericea L. (Det. R.B.B.). Host, *Succisa pratensis*. Location, England. Fig. 28.

Internal anatomy of *Abia* strikingly similar to that of *Zaraea* except for the following:

- A 2. Four regions to mid-gut: (1), roughly comparable to that of *Zaraea*, one-sixth gut length, longitudinally and transversely striate, muscular region; (2), one-sixth gut length, smooth surface, effect that of large mosaic resulting from underlying cell outlines; (3), one-third length, six heavy folds, curved longitudinally, edges of folds delimited by single-cell crypt-like protuberances; (4), smooth to hind-gut. Middle third with deeply curved, longitudinal folds, approximately six in number, unlike large, curved, single typhlosole-like fold of *Zaraea*.
- B. Malpighian tubule main stalks remain together, follow mid-ventral line for some distance, flat to leaf-like structure. Branches strap-like in appearance.

Trichiosoma triangulum Kirby. Host, *Salix*. Location, Ottawa, Ont., Canada. Fig. 31.

- A 1. Pharynx, narrow; oesophagus, enlarged; crop distinctly divided into regions by heavy muscular bands. Oesophageal invagination present.
2. Mid-gut, four regions: (1), strong muscular bands with peculiar longitudinal striations unlike the purely circular striations in *Cimbex*; (2), as in latter, characterized by scattering of crypt-like single-celled protuberances, uniformly distributed; (3), dense scattering of crypt-like cells; (4), smooth.
- B. Two common stalks of Malpighian tubules enter mid-gut separately. Stalks so close at entrance as to suggest possibility of fusion and common entrance. Stalks directed anteriorly and slightly dorsally. Each branches

into approximately five main tubules, which in turn branch, extending anteriorly and posteriorly. All tubules re-branch. Posterior ones are bound perirectally.

- C. Single pair of main salivary glands, broad expansible ducts, gland cells in rows, two to four cells per cluster.
- E. Crescentic spiracular glands, large conical glandubae.

Cimbex americana americana Leach. Host, *Salix*. Location, Ottawa, Ont., Canada. Figs. 29, 140.

- A 1. Pharynx, narrow; oesophagus enlarged into thick, muscular crop; wide oesophageal invagination projecting into mid-gut lumen.
- 2. Mid-gut divided into four regions: (1), slightly less than one-eighth gut length, thick muscular fold over sphincter region; (2), less than one-quarter length, possesses scattering of crypt-like protuberances, single-celled, fairly widely spaced over first half, densely packed over last half; (3), very widely separated crypt-like cells, extending half length of gut, delimited posteriorly by ring of extremely prominent gastric diverticula, irregular in size and shape, projecting in five clumps; (4) extends from diverticula to hind-gut, loosely longitudinally folded, superficially smooth.

Histologically slight, gradual transition from columnar to flat epithelial cells from region of diverticula. Epithelial cells uniform posteriorly. Single-celled crypt-like protuberances have "cilia" projecting into lumen formed by cell everted through the abdominal muscle sheath, the neck constricted by the muscles themselves. Mid-gut epithelial cells possess "cilia" almost as long as cell. "Cilia length" emphasized in descriptions of adult *C. americana* (58, 59). Peritrophic membrane single, thick layer, possibly fused.

- 3. Ileum, large; colon distinct; rectum very large.
- B. Six common stalks of Malpighian tubules enter separately mid-ventral region of mid-gut. Two stalks slightly anterior, two slightly posterior, and two between. Main axis of two anterior stalks parallel to mid-ventral line, directed anteriorly, branching into approximately ten Malpighian tubules each, these branching in turn. Tubules extend somewhat latero-dorsally and anteriorly, floating freely in the body cavity. Main axes of two posterior stalks, also parallel to mid-line, are directed posteriorly, branching into ten Malpighian tubules, which extend latero-dorsally and posteriorly, some floating freely, others bound perirectally. Main axes of two small intermediate stalks perpendicular to mid-ventral line. Slender stalks extend latero-dorsally each branching into two or three tubules, which divide in turn, floating freely in the body cavity. Approximately 100 tubules in all. The posterior stalks and branches of *C. americana* resemble the Malpighian tubule arrangement found in *Arge pectoralis*, indicating, perhaps, that the two species have reached almost the same stage of advancement and are both fairly specialized sawflies.
- C. Salivary glands, single pair of main, small pair of accessory. Main ducts large, expansible, coiled ducts extending length of body. Gland cells much smaller than the cluster cells of *Arge*, individually attached to main duct, form two single rows of cells along the length. Indications of cells clumping anteriorly by twos or threes before joining the duct, "diprionid-like" salivary.

- D. Fat body composed of peripheral fat sheath, separate thick layer of fat cells around Malpighian tubules and rectum, (Eliescu, 22).
- E. Body surface conspicuously spotted with oval to round swellings much larger than typical sawfly glandubae. Hollow spine in centre of each protuberance suggestive of glandular function. Some sections show large glands just beneath epidermis, similar in size to protruding glands. Numerous clusters of cells from common stalks project into lumen of glands, not reminiscent of argid ventral glands since two cell types in the latter. Crescentic subspiracular glands present in *Cimbex*; on histological section, structure similar to large glands mentioned above.
- F. Cuticle thrown into innumerable low to knob-like projections, apparently raised portions of endocuticle, capped by thin layer of epicuticle. Black mid-dorsal stripe, a striking distinguishing feature of *Cimbex* larvae, consists of rows of black spines shaped like arrow-heads, separated by colourless cuticular strip and deeply embedded in the cuticle.

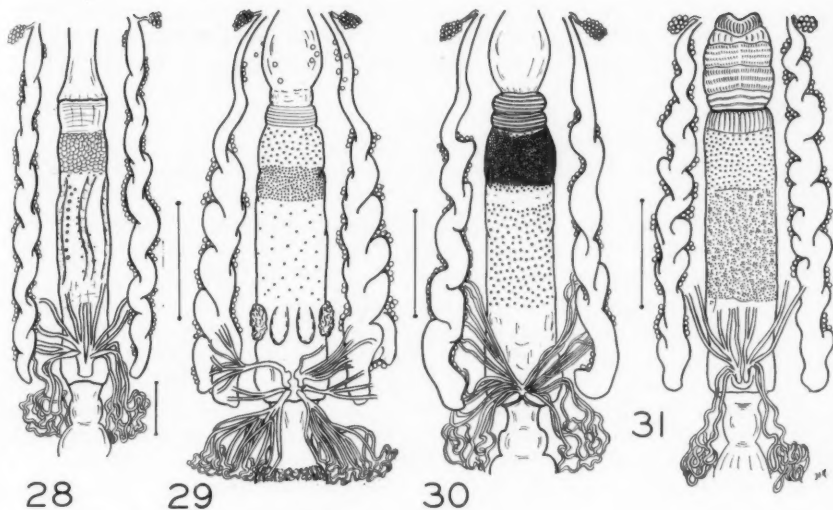
Cimbex sp. Host, *Ulmus americana* L. Location, Sault Ste. Marie, Ont., Canada. Fig. 30.

Berland (9) has made use of the dark-stripe character in some species separations of European cimbicids.

In the course of examining larvae of *Cimbex*, one group of elm feeders with a solid black stripe down the dorsum, unlike *americana americana* (where the black stripe faintly but distinctly splits), and with the prothoracic segment joined rigidly to the head capsule (as opposed to a constricted neck in *americana americana*) were found to lack gastric diverticula completely, and to show an interesting Malpighian tubule fusion.

- A 2. Mid-gut extends dorsally in a posterior bulge beyond limits of junction of hind- and mid-gut; four regions: (1), about one-sixth length of gut, two thick muscular folds over sphincter region; (2), about one-fifth length, tightly packed, crypt-like cells protruding, giving surface a pebbled plushy effect; (3) half length of gut, more widely spaced, crypt-like cells, clear anteriorly; (4), smooth.
- B. Malpighian tubules enter large, common duct mid-ventrally, which forms a collar about mid-gut at junction with hind-gut. The general arrangement of tubules follows the *C. americana* pattern with the added feature that some of the tubules are superimposed on others. Secondary branching occurs, totalling over 100.
- C. Salivary glands as in *C. americana americana*.

Benson (7) describes the Cimbicidae as a small family with less than 130 known species in 19 genera and four subfamilies. He says "The systematics of some of the genera of this subfamily, notably *Cimbex* and *Trichiosoma*, are notoriously difficult, with trouble not in the absence of characters to work on but in extreme individual variability in nearly all structural characters so far examined On the surface it would appear that a number of different species of *Cimbex* and *Trichiosoma* exist, and that these can be readily distinguished on biological characters, larval form correlated with host-plant. Some of them appear to be geographical races". He advocates intensive work with bred material, and says that until such material is available present-day keying should be viewed with suspicion. Ross (52) stresses that the genera *Cimbex* and *Trichiosoma* contain several nearctic species all in need of intensive study to ascertain species limits. Yuasa (69) emphasized that systematists agreed at least to the generic level in the cimbicids, which he placed among the first



Figs. 28. *Abia sericea* L. 29. *Cimbex americana americana* Leach. 30. *Cimbex* sp. 31. *Trichiosoma triangulum* Kirby.

subfamilies of his Tenthredinidae, between the Tenthredininae and the Hoplocampinae. He considered *Cimbex* the primitive genus in his Cimbicinae, with *Trichiosoma* and "*Abia*" (= *Zaraea*) more advanced forms. Ross (52), on the contrary, discusses the forms in the order *Zaraea*, *Trichiosoma*, and *Cimbex*.

The Malpighian tubule arrangement in *C. americana* indicates a highly advanced level in comparison with other sawfly families; more species in this group should, however, be examined before the relative positions of the species can be determined. There is a neat gradation in tubules in the five forms studied (see Table 9). The posteriorly-directed stalks of *Cimbex* show a greater or lesser degree of specialization than the entirely anteriorly-directed stalks of *Zaraea*. On the assumption that a trend towards posterior orientation and perirectal binding is one towards specialization, the writer believes that the internal anatomy results corroborates Ross' sequence (52). Increased complexity in crypt-like protuberances and diverticula from *Zaraea* to *Cimbex* may be a response to the differences in size of the larvae compared.

Malaise (39) divided the Cimbicidae, his "Cimbicinae", on the character of the fore-wing anal cell, into two tribes, the Cimbicini and Zaraeini. Ross (52) states the differences between them are insufficient to warrant the division. Benson (4) divides the Cimbicidae into four subfamilies of which three are restricted to the north temperate regions and tropical Asia: the Cimbicinae comprising the Cimbicini and Trichiosomini; the Abiinae comprising the Zaraeini and Abiini; and the Coryninae. The fourth subfamily and the Pachylostictinae are restricted to South America. The few species examined so far, point to great homogeneity in the Cimbicidae, which makes imperative the examination of other subfamilies, as well as additional species in those already studied.

Yuasa emphasized the odd, yet interesting fact that Konow (36) had once included the Perginae in the subfamily Cimbicinae. On the basis of the anatomy

of *Perga* and *Cerealces*, there is nothing incongruous in the grouping since either form would fit more logically into the Cimbicidae or Diprionidae than into the other groups included in the generally argid-like pergid complex.

Family Diprionidae

Subfamily Monocteninae

Monoctenus juniperinus MacG. Host, *Thuja occidentalis* L. Location, Ottawa, Ont., Canada. Fig. 32.

- A 1. Pharynx, narrow; oesophagus, short, round, followed by large transversely striate crop. Two capacious, thin-walled oesophageal pouches extend from oesophagus beyond third thoracic segment.
2. Mid-gut, two regions: (1), half total length of gut, no pronounced longitudinal folds, held distinctly away from oesophageal invagination by cardiac sphincter muscles, trace of longitudinal folding at end of region, possibly indicative of crypt regions in other Diprionidae; (2), same transverse striations as crop. Mid-gut proportions relative to those of fore- and hind-gut reduced in *Monoctenus* as compared with other species. Here mid-gut less than twice length of fore-gut. No histological peculiarities except a persistent hyaline layer immediately below the "ciliated" fringe in epithelial cells.
3. Large rectum. Two rows of chitinous rectal teeth embedded in cuticular lining of epithelium of colon and rectum.
- B. Ten separate, evenly spaced Malpighian tubules enter gut. Each tubule directed short distance anteriorly, coiling loosely posteriorly and bound perirectally.
- C. Salivary glands, single pair of main, small pair of accessory. Main ducts large, expansible, coiled tubes extending length of body. Gland cells in double rows along each side of duct. Glandular cells densely clumped anteriorly somewhat in manner of false reservoir.
- F. Cuticular layers thick, thrown into smooth lobe-like projections, endocuticle thickest. Not as in *Arge pectoralis* with epicuticular ridge or extra secretory layer, the smooth uniform lobes in *juniperinus* endocuticular, capped by a thin epicuticular layer.

MacGillivray (38) established a 'subfamily, Monocteninae, for the genus *Monoctenus* associating it with the Cladiinae and Nematinae. On the basis of his wing-venation criterion, this was justifiable, although contradicting previous workers, who stressed *Monoctenus* as a member of the Diprionidae (or Diprioninae). Yuasa was convinced that *Monoctenus* was a member of the Diprioninae, and anatomical results are in complete agreement on the basis of presence of oesophageal diverticula and structure if not proportions of the gut.

Subfamily Diprioninae

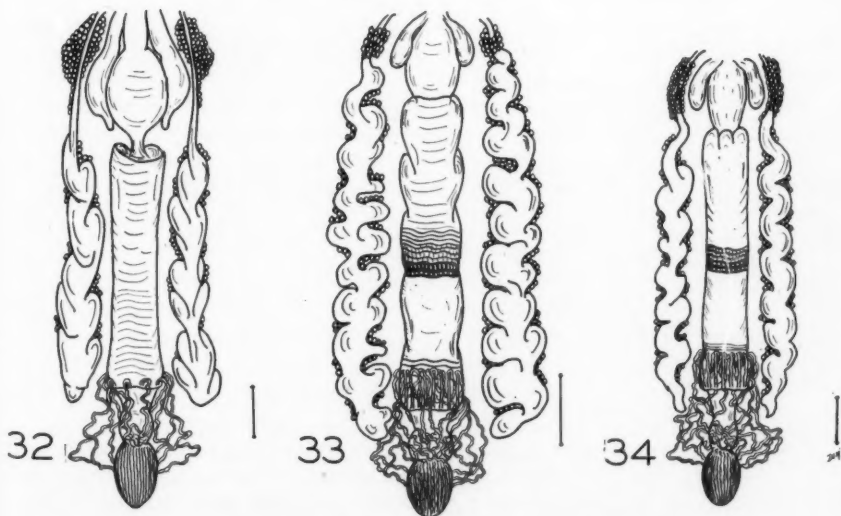
Neodiprion swaini Middleton. Host, *Pinus banksiana* Lamb. Location, Sault Ste. Marie, Ont., Canada. Fig. 33.

- A 1. Pharynx, narrow; oesophagus, pear-shaped, expansible into fairly large crop. Pair of thickly muscular oesophageal pouches or diverticula. In histological section, oesophageal invagination apparent, clear ovoid cells.
2. Mid-gut, three regions: (1), slightly over one-half gut length, deeply transversely striate, slight indication longitudinal foldings, delimited

posteriorly at approximately fourth abdominal segment by two rows of protruding crypt cells, four rows transitional crypt-like cells anterior to these; (2), extending to about three-quarters length of gut, smooth; (3), strongly, transversely striate to junction with hind-gut.

In histological section, uniform, columnar epithelium of region 1 gives rise to series of folds in crypt-like region. Slight histological differences apparent in regions 2 and 3, with a gradual transition from a cylindrical cell-type to a more columnar type. The peritrophic membrane extends from a "press" region between the anterior cells of the mid-gut and the lateral flaps of the oesophageal invagination. Thick membrane possibly consists of several closely adhering layers.

3. Two rows rectal teeth present, one each in colon and rectum.
- B. Approximately 28 separate, evenly-spaced tubules enter the mid-gut, each tubule extending approximately one-seventh or one-eighth of gut length anteriorly, turns, coils loosely posteriorly, and is bound perirectally.
- C. Salivary glands, single pair of main, small pair of accessory, essentially similar to those of *M. juniperinus*. Gland cells form two single rows along length of duct, separate entrance, *contra* Saint-Hilaire's (54) description of two cells per small branch-duct.
- D. Fat body thick, cells smaller in peripheral region and larger in main body sheath. As described by Eliescu (22) in *L. pini*, three regions to main body sheath: a sheath around the abdominal tract, binding the gonads and salivaries to the gut; one around the Malpighian tubules, colon and rectum; and a smaller, separate sheath, around the rectum.
- E. Occasional glandubae found scattered about the cuticular surface.
- F. Cuticle fairly thick, endocuticle with thin epicuticular layer. Rounded spines embedded in the cuticle.



Figs. 32. *Monocteus juniperinus* MacGillivray. 33. *Neodiprion swainei* Middleton. 34. *Neodiprion abietis* (Harris).

Neodiprion abietis (Harris). Host, *Abies balsamea* (L.) Mill. Location, Ottawa, Ont., Canada. Fig. 34.

Mid-gut marked anteriorly by approximately six deep longitudinal folds, faintly striate to the crypt-like region, three anterior rows transitional type, two posterior with actual crypt-like protuberances, latter multicellular, not unicellular as in *Cimbex*.

Neodiprion lecontei Fitch. Host, *Pinus resinosa* Ait. Location, Ottawa, Ont., Canada. Fig. 35.

- A 2. Anterior half of mid-gut deeply, longitudinally marked into six folds, heavily transversely striate to crypt region. Nine rows in various stages of transition near mid-point followed by four rows of crypt-like protuberances. Following gut region smooth to posterior area of transverse striation.

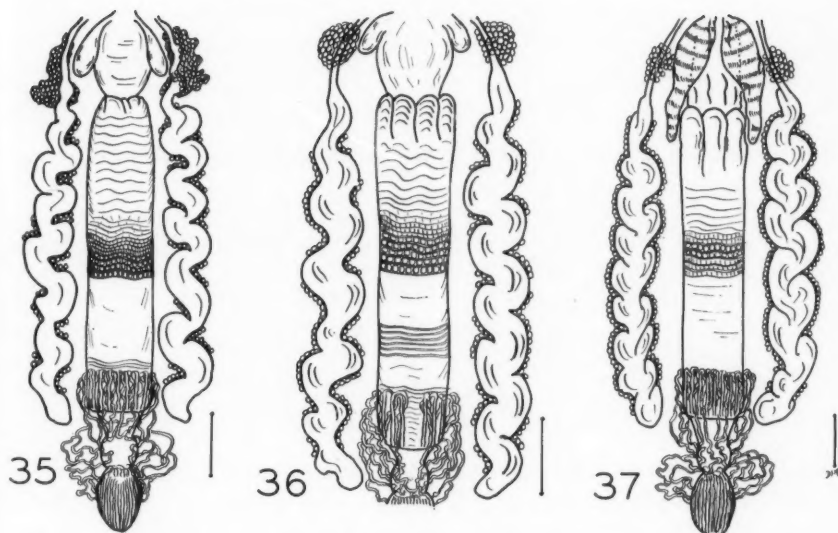
Other members of the genus *Neodiprion* examined were *N. burkei* Middleton, *N. nanulus* Schedl, *N. sertifer* Geoffroy, *N. tsugae* Middleton, *N. americanus americanus* (Leach), *N. americanus banksianae* Rohwer, *N. americanus dyari* Rohwer, *N. pinetum* (Norton), and *N. virginiana* Rohwer. The general anatomy of all the species of *Neodiprion* is monotonously similar; differences found on a minor level are here described for *swainaei*, *abietis*, and *lecontei*. An analysis of the rectal teeth patterns as a means of separating the species in the Diprionidae will be described by the author in a separate communication. Ross' (53) division of the "*Neodiprions*" into "groups", e.g. the *Swainaei* Group, *Abietis* Group, and the *Lecontei* Group, is still tentative, based for the most part on adult female saw types, and corroborated by general larval types.

Diprion (Diprion) similis (Hartig). Host, *Pinus sylvestris* L. Location, Ontario, Canada. (Introduced) Fig. 36.

- A 2. Mid-gut with five regions: (1), slightly over half the length of gut, carved longitudinally into six prominent folds, deeply transversely striate, posterior end with five anterior transitional rows and five rows of crypt-like protuberances; (2), smooth, similar to, but shorter than (3) of *Neodiprion*; (3), transversely striate; (4), smooth to area reached by Malpighian tubules; (5), finely transversely striate. Histologically mid-gut cells relatively uniform in size and shape, becoming taller and more columnar towards junction with hind-gut.

Diprion (Gilpinia) hercyniae (Hartig). Host, *Picea glauca* (Moench) Voss. Location, Ottawa, Ont., Canada. (Introduced) Figs. 37, 141.

- A 1. Pharynx, narrow; oesophagus, enlarging into fairly extensive crop; pair of extremely large oesophageal pouches extending as far as first and second abdominal segments. Walls of oesophageal pouches strongly marked by muscular ridges and rings. Histologically, two long oesophageal lateral flaps evident, no true oesophageal invagination such as found in *D. (D.) similis*.
2. Mid-gut, three regions roughly comparable to those of *N. lecontei*: (1), slightly less than half length of gut, deeply longitudinally folded, folds flattened, projecting over oesophagus, posterior limits marked by five transitional rows and two rows of crypt-like protuberances; (2), smooth; (3), transversely striate from anterior bend of Malpighian tubules.



Figs. 35. *Neodiprion lecontei* (Fitch). 36. *Diprion (Diprion) similis* (Hartig). 37. *Diprion (Gilpinia) hercyniae* (Hartig).

Histologically, epithelium of region 1 thrown into series of shallow folds, cells tall and cylindrical. From fourth abdominal segment, epithelium projects through the muscles binding the gut into the body cavity in crypt-like formation, each "crypt" formed of two or three cells. Regions (2) and (3) have uniform columnar epithelium.

3. Two rows of rectal teeth, one each in colon and rectum.

B. Approximately 24 evenly spaced Malpighian tubules, distribution and direction as in *N. lecontei*.

Diprion (Gilpinia) frutetorum (Fab.). Host, *Pinus sylvestris* L. Location, Ottawa, Ont., Canada. (Introduced). Similar to *hercyniae* except crypt cells smaller, fewer transitional rows.

The crypt-like protuberances in both species of *Gilpinia* are more like small gastric caeca than those of the other *Diprionidae*. *D. (G.) pallida* (Klug) was examined in England, and found to be internally similar to the preceding two species.

Ross (53) recently made *Diprion* and *Gilpinia* subgenera within the genus *Diprion*, whereas Benson (7) retained their generic status. The similarity between *Diprion* and *Gilpinia* is no greater than that between *Neodiprion* and either of these, so that it would seem more logical to maintain a generic status for all three than to create one or more subgenera.

The family *Diprionidae* is imperfectly understood. Adults are very similar, frequently almost indistinguishable even upon fine genitalic characters. There is apparent synonymy in some cases and a need for further separation in others. The larvae are equally confusing. Obviously, speciation in this family is incipient. The need for stable characters of specific significance, both larval and adult, is self-evident.

Family Tenthredinidae

Subfamily Selandriinae

Tribe Strongylogasterini

Hemitaxonus dubitatus (Norton). Host, *Osmunda* sp. Location, Ottawa, Ont., Canada. Fig. 38.

- A. 1. Pharynx, narrow; oesophagus, bulbous, expanding into fairly large crop.
 2. Mid-gut uniformly thick tube.
 B. Eight Malpighian tubules, six ventral, evenly-spaced, extending anteriorly, floating freely in the body cavity; two relatively wide tubules close to mid-dorsal line, extending laterally around gut, may entwine ventral tubules, turning posteriorly, loosely attached perirectally.
 C. Salivary glands, single set of main, one of accessory branching from posterior end of salivary reservoir. Main duct extends as narrow tube, widening in series of bulb-like expansions alternating with narrow portions of duct. Single row of individually attached gland cells each side of duct.

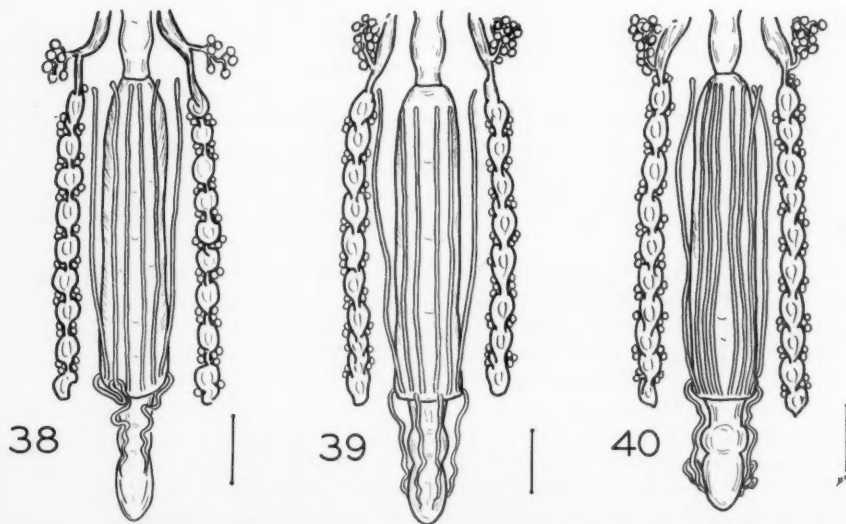
Hemitaxonus sp. 1. Host, *Pteris* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 39.

- B. Ten Malpighian tubules, eight ventral, two dorsal. Six ventral tubules extend anteriorly at evenly-spaced intervals as in *dubitatus* but one posteriorly directed tubule is interposed between the first and second ventrals on each side the mid-ventral line. The two dorsal tubules as in *dubitatus*.

Hemitaxonus sp. 2. Host, *Pteris* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 40.

- B. Fourteen Malpighian tubules, eight ventral, four ventro-lateral, two dorsal. Twelve extend anteriorly, at evenly-spaced intervals; 2 dorsal tubules, laterally around the gut as in previous two forms.

The three forms varied in external larval markings.



Figs. 38. *Hemitaxonus dubitatus* (Norton). 39. *Hemitaxonus* sp. 1. 40. *Hemitaxonus* sp. 2.

Ross (52), describing the hypothetical adult ancestor for the Tenthredinidae says that the conditions postulated are found only in some specimens of the genus *Hemitaxonus*, but are approached by most genera in the subfamily Selandriinae. From this stage, steady evolution along several diverse lines led, Ross believes, to the specialized groups, the Nematinae, Tenthredininae, and Allantinae.

Strongylogaster tacitus (Norton). Host, *Pteris* sp. Location, Ottawa, Ont., Canada. Fig. 41.

- A 1. Pharynx, narrow; oesophagus, slender, enlarging into wide crop.
- 2. Mid-gut, two regions: (1) first half loosely folded and smooth; (2) strongly transversely muscular, anterior part characterized by series of deep longitudinal folds, lobe-like, reflected interiorly as inverted gastric caeca, or diverticula.
- B. Ten Malpighian tubules: four ventral, directed anteriorly, floating freely in body cavity; six dorsal, three evenly-spaced tubules either side mid-dorsal gap, innermost directed posteriorly, bound perirectally, remainder extending short distance posteriorly, turning anteriorly, floating freely in body cavity.
- C. Salivary glands, single pair main, small pair accessory. Main ducts alternate in diameter. Anterior part lacks glandular cells, slightly enlarged reservoir, not so pronounced as in *Hemitaxonus*. Gland cells uniformly spaced in rows along duct, four or five cells per clump entering in region of bulb-like expansion. Condition as described for *Selandria adumbrata* by Saint-Hilaire (54). Gland cell shape somewhat flattened cuboidal, with definite stalk.

Strongylogaster macula (Klug). (Det. R.B.B.). Host, *Pteris* sp. Location, Scotland. Fig. 42.

Species strikingly similar in internal anatomy to *Hemitaxonus dubitatus*.

- A 1. Pharynx and oesophagus slender, latter expanded into very large thin-walled crop, approximately one-third the length of the mid-gut.
- 2. Simple unmodified tube.
- B. Average number of tubules nine; six ventral, anteriorly extending, three dorsal, with the two outermost swinging laterally to ventral surface as in *H. dubitatus*, then posteriorly, bound perirectally. Third dorsal tubule extends posteriorly from the mid-dorsal line. The first case of variation in Malpighian tubules of what is commonly recognized as one species was found in *macula*. The average number of tubules is nine, but in a group of approximately 20 larvae two extra anteriorly extending tubules were observed five times: resulting in eight ventral and three dorsal tubule arrangement.
- C. Salivary glands, single set of main, single pair accessories off anterior reservoir. No gland cells until region of ducts posterior to the reservoir. Clumps of two or three cells entering ducts which consist of alternate narrow junctions and bulb-like expansions.

Tribe Aneugmenini (of Benson)

Aneugmenus sp. (Det. R.B.B.). Host, *Pteris* sp. Location, England. Fig. 44.
(included in the *Strongylogasterini* by Ross).

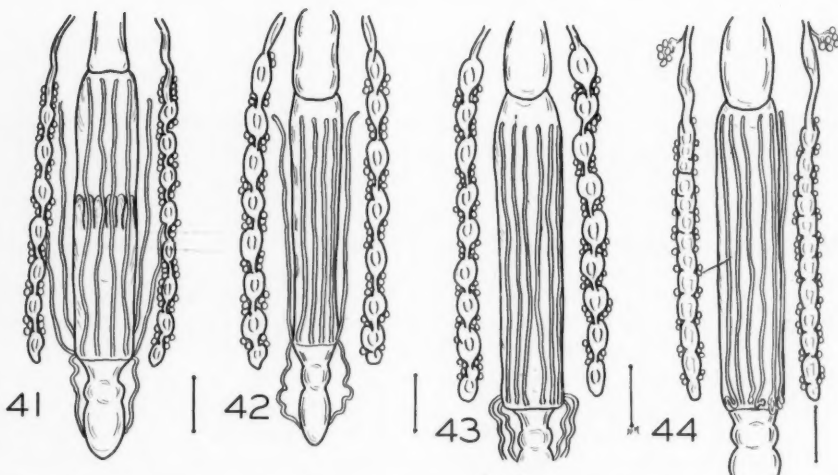
- A 1. Crop huge, extending to third thoracic segment.
- B. Twelve Malpighian tubules: six ventral, extending anteriorly; six dorsal, extending posteriorly.

- C. Typical segmented gland but a telescoped squared type. Individual attachment of squared gland cells. No reservoirs, accessory gland off slender anterior end of duct.

Tribe Selandriini

Selandria serva (F.). (Det. R.B.B.). Host, Gramineae. Location, England. Fig. 43.

- A 1. Pharynx, narrow; oesophagus, expanded into huge crop extending to third thoracic segment.
2. Mid-gut, broad unmodified.
- B. Ten Malpighian tubules; six ventral, evenly spaced, extending anteriorly; four dorsal, circling the gut to ventral surface, here extending posteriorly, bound perirectally.
- C. No reservoirs but set of main glands has alternating, narrow duct and bulb-like expansion, latter squared in appearance. Gland cells flattened cuboidal, tapered, joining duct individually or in clumps of two or three.



Figs. 41. *Strongylogaster tacitus* (Norton). 42. *Strongylogaster macula* (Klug). 43. *Selandria serva* (Fabricius). 44. *Aneugmenus* sp.

The salivary gland characters of the specimens examined support the tribal separation of the *Strongylogasterini* and the *Selandriini*, and possibly, the *Aneugmenini*.

As will be stressed later in the conclusion, the 10-Malpighian-tubule arrangement and simple alignment of the tubules, as well as the peculiar structure of the salivary ducts, presence of anterior reservoirs, and shape of gland cells are accepted as primitive characters in keeping with the theory that *Hemitaxonus* and *Strongylogaster*, at least, are close to the hypothetical tenthredinid ancestor.

Yuasa (69) considered the *Selandriinae* a fairly compact subfamily, containing a limited number of genera, larvae with larvapods on abdominal segments 2 to 8 and 10, seven annulets on the third abdominal segment, 5-segmented antennae, body uniformly greenish; head with or without brownish spots; wings

with a fairly standardized venation. On the basis of venation, MacGillivray (38) had placed the subfamily beside the Emphytinae. Yuasa agreed with Rohwer's (47) removal of *Hemitaxonus* and *Epitaxonus* from the Emphytinae on the basis that the two genera were characterized by setiferous larvapods and presence of seven annulets as in the Selandriinae rather than non-setiferous larvapods and six annulets as in the Emphytinae. Benson (7) and Ross (52) separate the two subfamilies widely. The former places the Emphytinae as the tribe Emphytini in his large Blennocampinae; the latter has Selandriinae as the subfamily preceding the Phylotominae and Nematinae in order of advance in the Tenthredinidae.

Subfamily Dolerinae (Tribe Dolerini within Benson's Selandriinae)

Dolerus (Dolerus) vestigialis (Klug). (Det. R.B.B.). Host, *Equisetum* sp. Location, England. Fig. 45.

- A 1. Pharynx, narrow; oesophagus expanding into long wide crop.
- 2. Mid-gut unmodified.
- B. Twelve ventral Malpighian tubules extend anteriorly, four dorsal posteriorly, looping ventrally around gut before curling posteriorly.
- C. Salivary glands, two main pairs, loose bulbous formation of ducts, no anterior reservoirs.

Ross (53) considers the forms known as *Dolerus* and *Dolerus* as subgenera of the genus *Dolerus*, since adult descriptions are exceedingly close for the two forms. Most other systematists tend to separate the two into distinct genera, as does Benson (7). External larval characteristics offer little, and the generally accepted adult separation character, "eyes emarginate mesally" for *Dolerus*, "eyes straight mesally" for *Dolerus* (52), is none too substantial a criterion for generic separation.

Dolerus (Dolerus) aericeps C.G. Thomson. (Det. R.B.B.). Host, *Equisetum* sp. Location, England. Fig. 46.

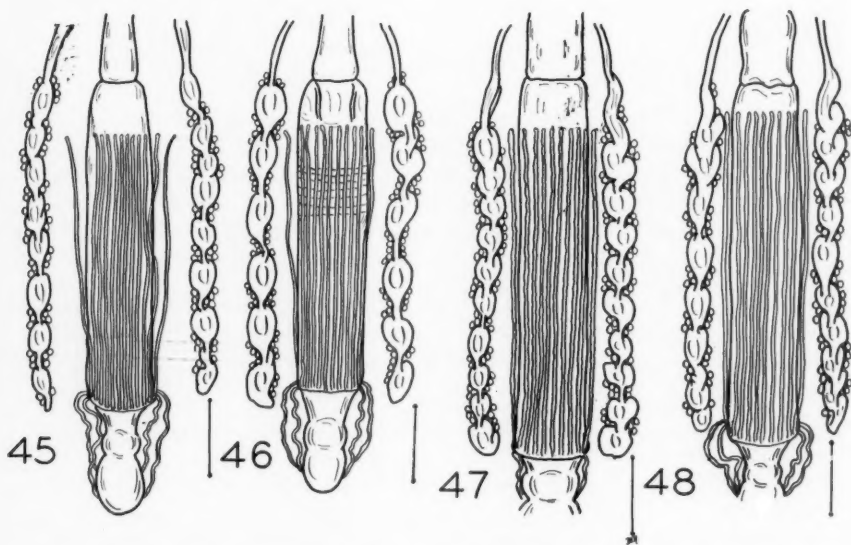
- A 1. Pharynx, narrow; oesophagus expanded into fairly large crop.
- 2. Mid-gut, three regions: (1) slightly under one-third length of gut, lightly marked into approximately six longitudinal folds; (2) a band of approximately five rows of deep transverse folds; (3) smooth to hind-gut.
- B. Sixteen Malpighian tubules enter mid-gut, 12 evenly-spaced, ventral, extending anteriorly; four dorsal, with mid-dorsal space, extending laterally to ventral surface, then posteriorly.
- C. Salivary glands, two sets main, alternation of fewer bulb-like expansions with narrow ducts as in *vestigialis* (and somewhat similar to *Strongylogaster*. Flattened, cuboidal gland cells, tapered ducts, no indication of reservoirs.

Dolerus cothurnatus Lepeletier. (Det. R.B.B.). Host, *Equisetum* sp. Location, England. Fig. 48.

- A 2. Mid-gut, unmodified, transversely striate to hind-gut, more deeply striate on anterior one-third.
- B. Eighteen Malpighian tubules: ten ventral, evenly spaced, extending anteriorly; eight dorsal, with mid-dorsal space, extending laterally about gut for some distance, then posteriorly.
- C. Salivary glands, two sets main, alternation of fewer-bulb-like expansions and narrow ducts, flattened cuboidal gland cells, no evidence of reservoir.

Dolerus triplicatus (Klug). (Det. R.B.B.). Host, *Juncus* sp. Location, England. Fig. 47.

- A 1. Pharynx, narrow; oesophagus expanded into extremely wide crop.
 2. Single row of rectal teeth in colon.
 B. Twenty tubules, 16 ventral, evenly spaced, extending anteriorly; four dorsal, with wide mid-dorsal space extending posteriorly, coiling laterally and ventrally, then posteriorly.
 C. Salivary glands, two sets main, slightly bulbous expansions to ducts, double rows of salivary gland cells.
 F. Cuticle, bubbled effect, resulting from minute raised papilla-like formation.



Figs. 45. *Dolerus (Loderus) vestigialis* (Klug). 46. *Dolerus (Dolerus) aericeps* C. G. Thomson. 47. *Dolerus (Dolerus) triplicatus* (Klug). 48. *Dolerus (Dolerus) cotburnatus* Lepeletier.

Yuasa (69) described the Dolerinae as a "well-defined subfamily with a distinct habitus . . . closely allied to the Emphytinae and Selandriinae". He believed a vein character, coalescence of cells R4 and R5 with atrophy of end of vein R5, to be the most important separation point of the Dolerinae from the other subfamilies. Larvapods are present, as in the Selandriinae, on segments 2 to 8 and 10, annulets unlike Selandriinae, six in number, labrum distinctly asymmetrical. Benson (7, 8) says of the Dolerinae "closely related to the Selandriinae with which they agree in the curving back of the base of the cubitus in the fore-wing towards the stigma; they are easily separated by the regular combination of four characters: prepectus absent, cervical sclerites meeting broadly in front, second cubital cross-vein absent and cross-vein to anal cell present in the fore-wing". Later Benson (8) incorporated one of what he terms his "radical changes" in his sawfly classification, the inclusion of the Dolerinae as a tribe in the Selandriinae,

impressed as he was, presumably, by the striking similarity in the two groups.

The salivary glands of the Dolerinae have the alternate bulb-like arrangement of the Selandriinae in general and the rounded bulbs of the Strongylogasterini; there are, however, two sets of glands and, as in the Selandriini, no reservoirs. Except for a doubling in the pair of salivaries, there is no indication of differences in the groups in question, and, as was seen within genera in the Argidae, an extra set of salivaries seems of little consequence. The Malpighian arrangement is strikingly similar, except for some differences in number in the two groups, an anteriorly extending row of tubules ventrally, and a few posterior tubules extending laterally from the dorsal surface around to the ventral in a wing-like formation. The general Malpighian similarity is accounted for either as an extreme case of parallel evolution in two neighbouring subfamilies or by the tribes being in the same subfamily and thus along the same line of descent. Anatomical details favour Benson's theory (7) that the tribes belong in the same subfamily, probably the most primitive in the Tenthredinidae, with the Dolerini a slight advance over the Strongylogasterini and close to the Selandriini. The host-plant association of the subfamily as a whole, Benson stresses, is with the Filicales, the few genera in the tribe Aneugmenini attached to herbaceous flowering plants being another indication of the primitive nature of the group.

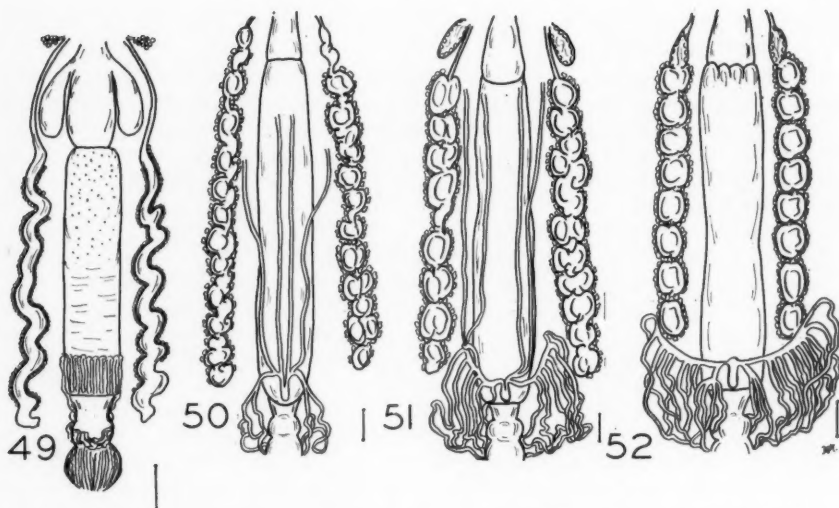
Subfamily Susaninae

Susana cupressi Rohwer and Middleton (Det. H.H.R.). Host, *Cupressus*. Location, Santa Susana, California, United States. Fig. 49.

- A 1. Pharynx, narrow; oesophagus, short, round, followed by large crop. Two huge oesophageal diverticula extend to beginning of mid-gut.
2. Mid-gut with two divisions: (1) approximately one-half length of gut, smooth, somewhat "pebbly" surface; (2) transversely striate.
3. Two rows rectal teeth present, embedded in cuticular lining of colon and rectum.
- C. Salivary glands, single pair of main, small pair of accessory. Gland cells individually attached.
- E. No ventral abdominal eversible glands.

Ross (52) originally placed the genus *Susana* in the Nematinae following *Hoplocampa* and *Caulocampus*. He remarked that the indication of the beginning of the middle tooth of the mandibles in *Susana* and in *Hemichbroa* seemed to point to an early branching from the Nematine stem. In his latest revision (53) the genus was granted subfamily status preceding the Nematinae, between the Dolerinae and the Heterarthrinae. Internal anatomical results favour the latter, emphasizing a special position for the Susaninae in close association with the Nematinae on the one hand, the Diprionidae on the other.

Except for the distance covered anteriorly by the Malpighian tubules (one-sixth gut length), the internal anatomy of *Susana* might well be mistaken for that of a diprionid (e.g. *Monoctenus* lacks any trace of crypt-like protuberances). The presence of oesophageal diverticula had hitherto been considered a property restricted to the Diprionidae, as the somewhat similar pharyngeal diverticula were to the Perginae. The oesophageal diverticula in *Susana* seem strong evidence of a close relationship to the Diprionidae. The larval antennae are five-segmented, raised, low-conical, tenthredinid in type, not the 4- to 5-segmented flat antennal type of the diprionid with a single raised spike. The



Figs. 49. *Susana cupressi* Rohwer and Middleton. 50. *Endelomyia aethiops* (Fabricius). 51. *Caliroa fasciata* (Norton). 52. *Caliroa cerasi* (Linnaeus).

intermediate-advanced Malpighian tubule arrangement characteristic of the Diprionidae and the Cladiini, Nematini and Pseudodineurini (Nematinae, Tenthredinidae) only is found in *Susana*, however, the absence of ventral abdominal eversible glands and presence of larvapods on abdominal segments 2 to 8 and 10, not 2 to 7 and 10, prevents the latter's inclusion in either of the two well-defined Nematine tribes.

Many sawfly workers have stressed the extreme similarity between the Diprionidae and the Tenthredinidae, as a whole, the Nematinae in particular. In 1918 Rohwer (48) stated "in a previous paper the writer had considered this group (Diprionids) of family rank but after studying the larvae and habits it seems that the group is so closely allied with certain subfamilies in the Tenthredinidae that it should be treated as a subfamily. Moreover, the differences between the Diprionids and the Tenthredinids is not of as much taxonomic value as the differences between the Tenthredinids and Argids or Cimbicids . . . The writer, therefore, prefers to consider the group as a subfamily of the Tenthredinids where it can be easily separated from the other groups by the multi-jointed antennae and the well defined dorsal plate of the mesoepimeron". Although, as will be emphasized in the discussion, an adjustment is needed in existing concepts of family and subfamily levels in the Tenthredinoidea, it is sufficient to mention that *Susana* fulfils to perfection the demands for characters of a hypothetical intermediate between the diprionids and the nematines.

Subfamily Heterarthrinae

Tribe Caliroini

Endelomyia aethiops (Fabricius). Host, *Rosa* sp. Location, Ottawa, Ont., Canada. Fig. 50.

- A. 1. Pharynx, narrow; oesophagus expanded into slight crop.
2. Mid-gut uniformly stout tube.
- B. Common stalk enters mid-gut, branches anteriorly into three main tubules on each side, two innermost extending anteriorly, outer tubule turns

posteriorly, rebranching about beginning of hind-gut. Posterior tubules bound perirectally.

- C. Salivary glands, single pair main, small pair accessory. Anterior reservoirs, duct alternating series of narrow junctions and bulb-like expansions. More telescoping of expansions in *Endelomyia* than in *Selandriinae*, i.e. junctions or narrowed portions comparatively shorter. Gland cells flattened cuboidal shape, entering duct individually or in groups of two.
- E. No eversible cervical or thoracic glands.
- F. Conical tubercles on dorsum of thorax and anal segment (*Dimorphopteryx*-like).

Caliroa fasciata (Norton). Host, *Crataegus* sp. Location, Ottawa, Ontario, Canada. Fig. 51.

- A 1. Pharynx, oesophagus, narrow; fairly large crop.
- 2. Mid-gut, unmodified, except for narrow, crescentic, muscular area anteriorly.
- B. Common stalk enters mid-gut, directed anteriorly, branches into three parts, median branch continues anteriorly divides into two tubules, each floating freely in body cavity. Each side branch extends latero-dorsally, partially encircling mid-gut as lateral wings floating freely, dorsally. From main part of each wing-like branch approximately five posteriorly-directed tubules given off, and at least two anteriorly directed.
- C. Salivary glands, single pair main, small pair accessory. Narrow main duct enlarged in series of bulb-like expansions, extreme telescoping, junctions almost non-existent. Two or more double rows of individually attached salivary gland cells, flattened cuboidal in shape, elongate. No reservoirs.
- E. Ventral thoracic views indicate three pairs of glands in various stages of eversion. A single pair of cervical eversible glands on dorsal surface, (see Yuasa, 69). Suggestions of non-eversible series of pairs of "glands" between abdominal prolegs, not as in *Arge*.

Caliroa cerasi (Linnaeus). (Det. R.B.B.). Host, *Prunus* sp. Location, England. Fig. 52.

- B. Common stalk branches into 2 latero-dorsally directed "collecting wings". Each wing gives rise to (a) one main branch close to main stalk which divides into three or four tubules extending posteriorly and bound perirectally, and (b) a series of single posteriorly directed tubules rather unevenly spaced in threes and fours, (approximately eight or nine tubules per side not counting end of wing.) Dorsally six posteriorly directed tubules leave the gut at evenly-spaced intervals. Apparently no anteriorly directed tubules in *C. cerasi*.
- C. As in *C. fasciata*, three to four rows of gland cells, possibility not all individually attached.

The taxonomic status of the Heterarthrinae (approximately equal to the old Phyllotominae) has been unstable over the last decade or two. Yuasa's Phyllotominae consisted of two distinct tribes, the Phyllotomini and Phlebatrophini, the former with tarsal claws and six annulets, the latter without claws and two annulets (leaf miners). There were two general in his Phyllotomini, tadpole-like *Caliroa* and tubercle-covered *Endelomyia*. Prothoracic glands oc-

curred in the *Caliroa*. MacGillivray had considered the Phyllotominae to be one of the five generalized subfamilies in the Tenthredinidae, and Yuasa concurred. Rohwer (47), Konow (36), and Enslin (23) have, at different times, grouped *Caliroa* and *Phyllotoma* with the Hoplocampinae (containing *Hemichroa* and *Caulocampus*, among others).

Ross (52) describes the large Phyllotominae, consisting of *Caliroa*, *Phyllotoma*, *Fenusa*, *Profenusa*, *Scolioneura*, *Entodecta*, and *Metallus*. The genus *Caliroa* was considered the most generalized form in the group. (*Endelomyia* he considered a synonym of *Caliroa*).

Benson (4) made four distinct tribes within the subfamily: the Fenusini, Phyllotomini, Heptamelini, and Caliroini. His reasons for doing so were, first, the positive one, that the basal and first recurrent veins converge strongly towards the stigma in the fore-wing and, second, the negative one, that these groups did not belong "clearly" to any other subfamily.

Ross (53) changed the subfamily name to the Heterarthrinae, containing the Caliroini (with *Endelomyia* and *Caliroa*), the Heterarthrini, the Fenusini (with *Metallus*, *Messa*, *Profenusa*, *Setabara* and *Fenusa*) and the new Nefusini.

Benson (8) transferred the Heptamelini from the Heterarthrinae to the Selandriinae and fused the Blennocampinae and Emphytinae (Allantinae) with the Caliroini and Fenusini of the Heterarthrinae to constitute the enlarged Blennocampinae. He added that possibly *Heterarthrus* itself belongs in the same complex but retained it in a separate subfamily, the Heterarthrinae. Reference will be made again to the possibility of including at least the Caliroini in the "Blennocampinae complex".

In salivary gland structure, the Caliroini are strikingly similar to the Selandriinae. The alteration of narrow duct and bulb-like expansion in the Caliroini appears a telescope modification of the Selandriinae. Anterior reservoirs are present in *Endelomyia* but not in the two species of *Caliroa* examined. The interpretation of this fact depends upon the emphasis placed on the reservoir as a character of importance at a higher level (such as the salivary glands themselves) or as a salivary modification of importance at a lower evolutionary level (such as the Malpighian tubules). In keeping with the latter hypothesis, the Caliroini are just as close to the Selandriinae as are the Dolerinae (Ross' term). Either the two are exceedingly closely related and parallel evolution is showing at its best, or the tribe might be considered part of an enlarged Selandriinae. The three species are at a fairly advanced stage in Malpighian type. *Endelomyia* has the general arrangement of *Zaraea* or *Abia* in the Cimbicidae, and the common stalk and wing-like formation of the two species of *Caliroa* represent an advance over the *Endelomyia* arrangement in the form of superimposed lateral wings (see specialized condition of *Neurotoma* in the Pamphiliidae).

Tribe Heterarthrini (Heterarthrinae of Benson)

Heterarthrus nemoratus (Fallen). Host, *Betula payprifera* Marsh. Location, New Brunswick, Canada. Fig. 53.

- A 1. Pharynx, narrow; oesophagus enlarged into elongate, somewhat bulbous crop.
2. Mid-gut unmodified stocky. Well-developed peritrophic membrane apparently secreted by mid-gut epithelium.
3. Colon, slender bulbous.
- B. Slightly globular common stalk tubules, directed anteriorly, branches four times to right, three to left. Four extend anteriorly, three pos-

teriorly loosely bound perirectally. Of the two extending anteriorly on each side of the initial branching, one lies dorsal to the other.

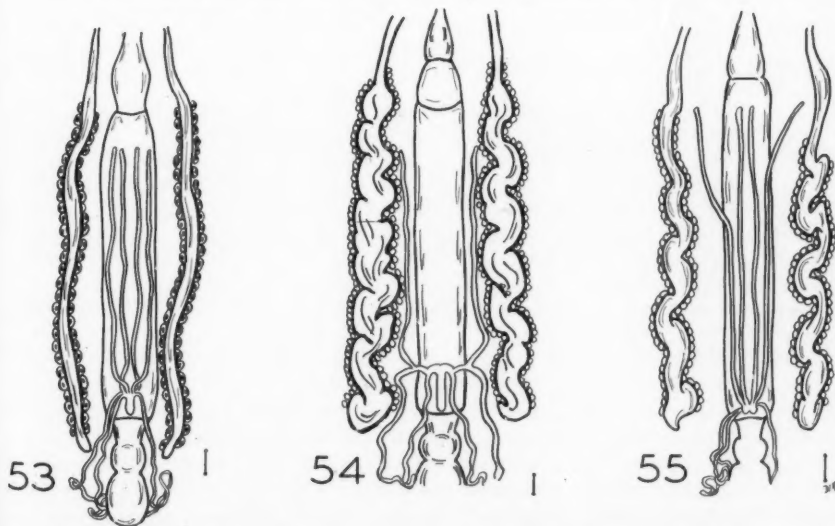
- C. Salivary glands, single pair of main, small pair of accessory. Ducts without indication of bulb-like expansion, extend as fairly wide straight expansible tubes. Gland cells in two rows bordering each duct and individually attached.

Benson (4) mentioned in his discussion of the Phyllotominae that the four tribes were distinct and might be regarded as separate subfamilies. He (8) retained *Heterarthrus* as the sole genus in a separate subfamily, the Heterarthrinae (=old Phyllotominae), admitting that *Heterarthrus* very likely belonged to his Blennocampinae complex as did the two tribes, the Caliroini and Fenusini. Benson describes the genus as a small one with primitive characters composed of leaf-mining species on trees of the Aceraceae, Betulaceae, and Salicaceae. Internally, the absence of salivary ducts with alternate bulb-like expansions and anterior reservoirs and the presence of advanced Malpighian tubule arrangement are not primitive characters. The duct type is that found in the Diprionidae and Cimbicidae and, as will be seen, in the Nematini of the Tenthredinidae. Once again either of two trends might be suggested: considering Ross' (52) palmate arrangement of sawfly subfamilies, the Heterarthrinae might lie between the Selandriinae and Nematinae or, in straight-line development, constitute an advance over the Selandriinae.

Tribe Fenusini

Parna tenella (Klug). (Det. R.B.B.). Host, *Tilia* sp. Location, England. Fig. 54.

- A 1. Pharynx, narrow; oesophagus, wedge-shaped; crop narrowly expanded.
2. Mid-gut short, squat, rectangularly-shaped tube. Anterior portion set off by muscles in rectangle.
B. Very long, slender, common stalk enters mid-gut, branches laterally left and right into two wide tubes in turn send off a posterior branch



Figs. 53. *Heterarthrus nemoratus* (Fallen). 54. *Parna tenella* (Klug). 55. *Metallus pumilus* (Klug).

immediately, and continue laterally to branch into two tubules, one extending anteriorly, the other posteriorly. Anterior tubules float freely, posterior ones loosely attached perirectally in fat sheath about hind-gut.

- C. Salivary glands, single pair of main with large expanded ducts, no trace alternate bulbs and narrow junctions. Thick rows of gland cells follow length of ducts, joining them by smaller ducts in clusters of two or three. Anterior region of ducts thickly covered with cells, false reservoir-like appearance.

Metallus pumilus (Klug). (Det. R.B.B.). Host, *Rubus* sp. Location, England. Fig. 55.

- A 2. Mid-gut rectangular shape as in *Parna*.
B. Two main, flask-shaped stalks fuse just before entering mid-ventral line. Each stalk sends off posteriorly extending tubule from lower half, two from the right stalk, one from the left. Anteriorly, each stalk divides into two anteriorly extending tubules floating freely in the body cavity.
C. Slightest hint of alternating diameters along the length of the duct. Intermediate stage between bulb-like expansions and straight tube type.

Metallus geii (Brische). (Det. R.B.B.). Host, *Geum* sp. Location, England. Fig. 56.

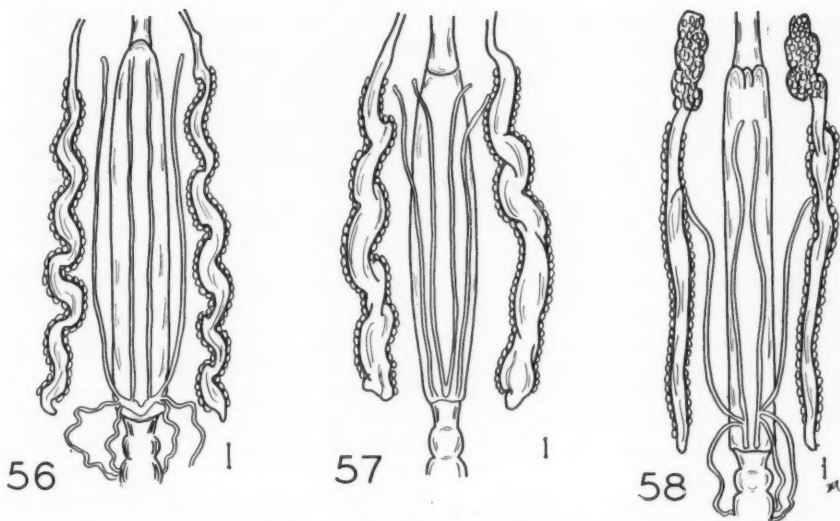
- A 2. Mid-gut as in two previous species. Oval flaps of mid-gut flattened, extended over fore-gut slightly.
B. Single entrance to large common tubule stalk on mid-ventral line. Two large stalks meet in a rounded V-formation, each tapering latero-anteriorly, single tubule off anteriorly near mid-ventral line, another as extension of tapered end. Two other tubules extend posteriorly from the common stalk. Lightly bound perirectally.
C. Salivary glands, single set of main, two single rows of individually attached salivary gland cells emptying into large, fairly uniform lightly curved ducts. Possible indication again of regular variation in diameter along the duct.

Fenusella (= *Profenusella*) *pygmaea* (Klug). (Det. R.B.B.). Host, *Quercus* sp. Location, England. Fig. 57.

- B. Three separate entrances for Malpighian tubules, two mid-ventral, anteriorly extending tubules fuse in a V-formation to enter gut; single anteriorly extending tubule enters ventral surface on either side. In all specimens indications of separate entrances for posteriorly extending tubule on the right, two on the left. The three extra tubules bound in the posterior body cavity, as if torn from indicated portions of the mid-gut.

Fenusella ulmi Sundeval. Host, *Ulmus americana* L. Location, Ottawa, Ont., Canada. Figs. 58, 142.

- A 2. Mid-gut anteriorly marked by approximately three flattened, oval, muscular extensions projecting somewhat over fore-gut (see *M. geii*).
B. Two separate entrances for tubules on either side mid-ventral line. Slender stalks, no wider than end of tubules. Each stalk branches, right into one posteriorly, and two anteriorly extending tubules; left into two posterior and two anterior.
C. Salivary glands, single pair, straight ducts, uniform. Anteriorly, accumulation of gland cells into what appears a false reservoir. Gland cells enter in twos.



Figs. 56. *Metallus geii* (Brische). 57. *Profenusa pygmaea* (Klug). 58. *Fenusa ulmi* Sundevall.

D. Internal organs encased in fat.

F. Cuticle characterized by smooth nodules, raised independently by underlying epidermal cells. Suggestion of "glandular space" between epidermal cells and nodule. Cuticle spiculate.

Fenusa dohrnii (Tischbein) and *Fenusa pusilla* (Lepeletier), leaf-miners of *Alnus* and *Betula* respectively, are strikingly similar internally, although the latter shows an interesting Malpighian variation. One main stalk enters the mid-gut, as in *Heterarthrus*, extending anteriorly, the stalk divides into two anterior tubules and a latero-dorsally extending tubule on the right, one anteriorly, one latero-dorsally on the left. The two laterals divide once more into anteriorly and posteriorly directed tubules. Hence, *Fenusa ulmi* and *F. dohrnii* have seven tubules, three on the right, four on the left (individual entrances in *ulmi*), whereas *F. pusilla* and *Heterarthrus nemoratus* have seven, four on the right, three on the left.

Yuasa (69) described his Fenusinae as consisting of four nearctic genera, closely allied to the Scolioneurinae and Blennocampinae. MacGillivray (38), one of the few others to grant the group subfamily rank, has stressed this fact. The larvopods of the *Fenusa* group are almost vestigial on abdominal segments 2 to 8 and obsolete on the anal segment (in *Heterarthrus*, a fused sucker-like larvopod on 10). Ross (52) included the *Fenusa* group in the Phyllotominae, and, in emphasizing the characters which he considered made *Caliroa* the most generalized component genus in the subfamily (bidentate mandibles and type of wing venation), described a trend from bidentate to tridentate mandibles, in the remaining leaf-mining forms, to the ultimate in venation reduction in *Fenusa*. Benson (4) described larvae of the Fenusini as possessing larvopods on abdominal segments 2 to 7 and 10, but examination of all available Canadian and British Museum material has shown that larvopods appear, at least in trace-form, on abdominal segment 8. Larvopods in both *Heterarthrus* and the *Fenusa* group are vestigial and merely mound-like in appearance. Benson agrees with a general

tendency to emphasize similarity of the *Fenus* group and the Blennocampinae and goes so far as to include it as a neighbouring tribe of the Blennocampini. Either of the two trends mentioned as possibilities for the Heterarthrinae, as compared to the Selandriinae and the Nematinae, might hold equally well for the Fenusini, which may be united with the Heterarthrini of Ross. The Malpighian tubules structure has reached approximately the same level in the Fenusini, Heterarthrini, and in *Endelomyia* of the Caliroini.

Subfamily Nematinae

Tribe Cladiini

Cladius isomerus Norton. Host, *Rosa* sp. Location, Ottawa, Ont., Canada. Figs. 59, 143.

- A 1. Pharynx, narrow; crop, transversely muscular, of three regions.
- 2. Mid-gut long, fairly stout, uniform tube; epithelial cells, with thick fringe of cilia and monotonously rectangular over length of gut, appear actively secretory in all regions; globules constricted off cells.
- B. About 28 evenly distributed tubules. Extend anteriorly for a distance approximately one-fifth length of mid-gut, turn posteriorly, firmly bound perirectally.
- C. Salivary glands three pairs of main. Inner pair, enlarged ducts slightly expandable even diameter, large gland cells varying in diameter from the same size as the duct, to twice the diameter, many cells typically flattened cuboidal with individual attachments. Outer ducts slender, identical, large gland cells about same size as inner cells.
- D. Peripheral and inner fat cells readily distinguishable.
- E. Ventral eversible glands between prolegs on abdominal segments 1 to 7.
- F. Long, vari-coloured seta-like hairs present. Hollow spines project through cuticle connected to specialized epidermal cells. Small spicules also projecting through cuticle.

Priophorus sp. Host, *Betula* sp. Location, Ottawa, Ont., Canada. Fig. 60.

- A 1. Pharynx, narrow; oesophagus expanding into slender muscular crop.
- B. Approximately 15 separate posteriorly extending tubules. Eight ventral tubules, middle four tubules swollen at entrance to gut. Seven dorsal tubules. All bound perirectally.
- C. Salivary glands, single pair gland cell clump anteriorly. Ducts divided into alternate bulb-like expansions and narrow junctions; gland cells enter duct individually, flattened cuboidal shape.
- D. Internal organs loosely banded by fat cells, no definite fat body regions.
- E. Ventral eversible glands present on abdominal segments 1 to 7.

The primitive salivary duct structure, and relatively low number and arrangement of Malpighian tubules, suggest this species occupies a fairly primitive position.

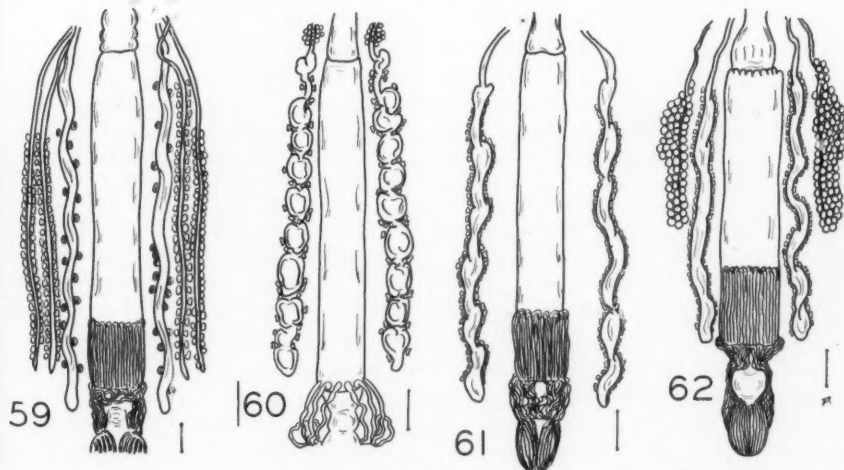
Priophorus morio Rohwer. Host, *Rubus* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 61.

- A 1. Pharynx, narrow; oesophagus enlarged into crop.
- 2. Mid-gut uniform tube to hind-gut.
- B. Twenty-two separate tubules. Each tubule loops anteriorly approximately one-fifth the length of gut, turns posteriorly, firmly bound perirectally.

- C. Salivary glands, single pair of main slight trace of bulb-like expansion, typically flattened cuboidal gland cells. No reservoirs.

Trichiocampus viminalis (Fallen). Host, *Populus tremuloides* Michx. Location, Ottawa, Ont., Canada. Fig. 62.

- A 1. Pharynx, narrow; oesophagus greatly expanded into muscular crop.
2. Mid-gut short stocky (in comparison to proportion of mid-gut in *Cladius*), set off anteriorly by pronounced longitudinal folds.
- B. A: proximately 28 separate evenly spaced tubules. Each tubule extends anteriorly approximately one-fifth mid-gut length, following far straighter course anteriorly than do the tubules of the Diprionidae. Tubules turn posteriorly and are loosely bound perirectally in the dorsal rectal region.
- C. Salivary glands two pairs of main present. Inner ducts similar to diprionid and other nematine ducts, two rows of gland cells (larger than diprionid) down each side of duct, individually attached, or in twos or threes. The gland cells typically flattened cuboidal type of the Selandriinae. (Saint-Hilaire describes a similar arrangement for *Cladius difformis*). The inner ducts have a peculiar cobbled surface effect. Outer ducts of greater diameter than inner, possess larger gland cells entering in clumps, anteriorly, and individually posteriorly. Gland cells closely packed almost covering ducts. It is doubtful that differences in phase of secretion could account for such extreme difference in the ducts.
- D. No indication of definite fat body regional distribution.
- E. Ventral eversible glands present on abdominal segments 1 to 7.



Figs. 59. *Cladius isomerus* Norton. 60. *Priophorus* sp. 61. *Priophorus morio* (Lepeletier). 62. *Trichiocampus viminalis* (Fallen).

Two other members of the Cladiini were examined:

Cladius pectinicornis Linnaeus. (Det. R.B.B.). Host, *Rosa* sp. Location, England.

- B. Twenty-two Malpighian tubules, slight mid-dorsal space apparent, strikingly similar to *Cladius isomerus*. Opening of tubules into gut in *pectinicornis* separate but in groups of two or three.

Priophorus pallipes Lep. (Det. R.B.B.). Host, *Crataegus*. Location, England.

- B. From 22 to 24 Malpighian tubules, directed anteriorly, as in other Cladiini, approximately one-sixth gut length, slight grouping in tubules.

Table 4 summarizes the arrangements of the Malpighian tubules and salivary glands in the Cladiini.

TABLE IV
Internal Anatomy Summary of the Cladiini

Species	Malpighian Tubules	Salivary Glands
<i>Cladius isomerus</i>	28	3 sets, 1 set trace expansion flattened cuboidal cells
<i>C. pectinicornis</i>	22-24	3 sets, 1 set trace expansion flattened cuboidal cells
<i>Priophorus</i> sp.	15	1 set, alternate expansions, flattened cuboidal gland cells
<i>P. morio</i>	22-24	1 set, trace expansion flattened cuboidal cells
<i>P. pallipes</i>	22-24	1 set, trace expansion flattened cuboidal cells
<i>Trichiocampus viminalis</i>	28	2 sets, 1 set trace expansion flattened cuboidal cells

Ross (52) stated that the "Cladiinae" were remarkably similar in many characters to the "Nematinae" but appeared to be a distinct, separate offshoot of the nematine stem. In his recent revision (53) the characters assume greater importance, from the point of view of considered similarity, and the subfamily is granted tribal status within the Nematinae.

MacGillivray (38) considered the "Cladiinae" to consist of six genera: *Caulocampus*, *Anoplonyx*, *Platycampus*, *Priophorus*, *Cladius*, and *Trichiocampus*. Rohwer (47) on the contrary, placed the first three in his Hemichroini of the Nematinae, stressing extreme dissimilarity in form between *Caulocampus* and *Priophorus*, dissimilarity to a degree indicative of a subfamily difference.

The observed absence of anterior reservoirs, presence of the Selandriinae-type flattened cuboidal cell, and a slight trace of alternate narrowing and expanding of the ducts, indicate a fairly primitive salivary type, generally similar to that of two genera in the Fenusini, and almost at the level of a straight duct type. If it were not for two particular characters of the Cladiini, it would be simple to assign this group to another branch in a "Selandriinae-Heterarthrinae-like complex". However, the presence of larvopods on abdominal segments 2 to 7, and 10, and of ventral abdominal eversible glands on abdominal segments 1 to 7, point to an exceedingly close association with the Nematinae. The Cladiini tubule arrangement is also strikingly similar to that of the Nematini. The large number of Malpighian tubules indicates an advanced stage, and the separate arrangement of entrances, resembles that of the Diprionidae.

Tribe Nematini

Hoplocampa testudinea (Klug). (Det. H.H.R.). Host, *Malus* sp. New York, United States. Introduced. Fig. 63.

- A 1. Pharynx, slender; oesophagus extensible into huge thin-walled sac into third abdominal segment.
- 2. Mid-gut short, stocky, transversely striate, first half; marked with deep longitudinal folds, almost typhlosole-like second half.
- B. Twelve Malpighian tubules. Separate entrances to mid-gut, indication of mid-ventral space. Irregular distribution anteriorly, all coil posteriorly, bound perirectally.
- C. Salivary glands, single pair of main, small pair of accessory. Gland cells individually attached. No indication of alternate bulb-like expansions and narrow junctions.
- E. Ventral abdominal eversible glands on segments 1 to 7.

Ross (52) regarded the genus *Hoplocampa* as the most primitive one in the Nematinae. An interesting trend is apparent from the characters e.g., wings and genitalia, of *Hoplocampa* through those of *Hemichroa*, *Anoplonyx*, and *Platycampus* to the more specialized Nematines such as *Pristiphora*, *Nematus*, and *Euura*. Internal anatomy confirms the primitive position of *Hoplocampa* within the Nematini and its close relationship with *Anoplonyx*.

Caulocampus acericaulis (MacGillivray). Host, *Acer saccharum* Marsh. Location, Ottawa, Ont., Canada. Fig. 64.

- A 1. Pharynx, slender, tapering; oesophagus fairly expansible.
- 2. Mid-gut, slender, unmodified tube.
- B. Six Malpighian tubules; two ventrally, directed anteriorly approximately one-third own length, turn posteriorly, ventro-laterally, each side of mid-gut, two tubules, one extending anteriorly, other posteriorly. General arrangement of tubules comparable to that of *Strongylogaster tacitus*.
- C. Salivary glands, single pair of main, small pair of accessory. Main ducts coil length of body, trace of alternation in diameter somewhat as in Cladiini. Rounded unmodified gland cells, join main duct in groups of two or more.
- D. Fat sheaths around internal organs, no definite organization noted.
- E. Eversible glands present on venter of abdominal segments 1 to 7. Trace of eversible on third thoracic segment.

The position of the genus *Caulocampus* has varied in accordance with the prevailing concepts of different workers. MacGillivray (38) included it in the Cladiinae and, as already mentioned, Rohwer (47) separated it in the tribe Hemichroini. Ross (52) and Yuasa (69) place it close to *Hoplocampa*; the former among the more primitive Nematines, and the latter as a member of a primitive subfamily in his Tenthredinidae. On the basis of its primitive Malpighian arrangement, the intermediate characters of the salivaries, and additional adult and larval characters, *Caulocampus* could be a generalized member of either the Cladiini or Nematini.

Hemichroa crocea (Fourcroy). Host, *Alnus* sp. Location, Ottawa, Ont., Canada. Fig. 65.

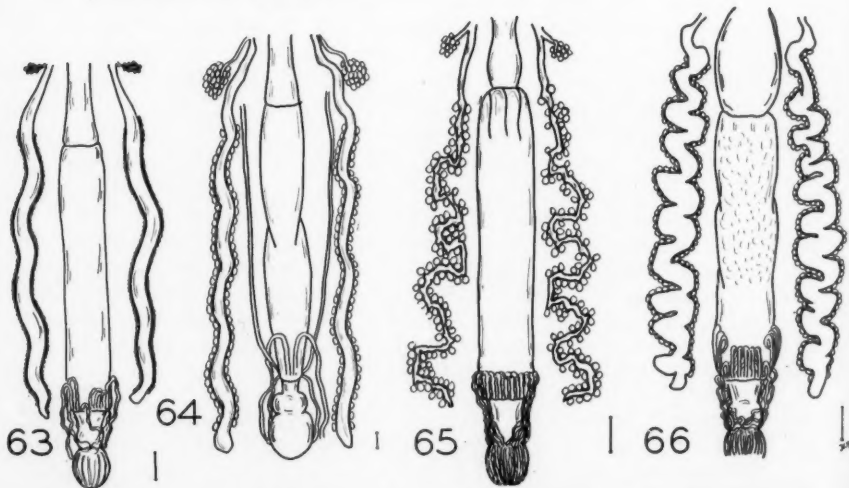
- A 1. Pharynx, narrow; oesophagus extensible into large crop (to about second thoracic).
- 2. Mid-gut short, stocky, delimited anteriorly by series of longitudinal folds.

- B. Approximately twenty-eight tubules enter gut separately. Each tubule extends shorter distance anteriorly than does one of the Cladiini, about one-twelfth length anteriorly, anterior loop greater in diameter than posterior loop. Tubules bound perirectally. This is a typical "nematine" arrangement.
- C. Salivary glands, single pair of main, small pair of accessory. Peculiarly irregular duct outline in collapsed state, possible indication of light alternations in duct diameter. Gland cells clump along either side of duct, compact clusters, four or five emptying together by small common ducts.
- E. Ventral eversible glands on abdominal segments 1-7. Tiny cask-like glandubae scattered about cuticular surface. Conical protuberances visible externally, some topped by spines. Different sized spines embedded in cuticle.

MacGillivray's (38) Hoplocampinae contained five genera, among them, *Hoplocampa* and *Hemichroa*. These with the Dineurinae made up a series of species with anal veins modified before the loss of radial cross veins. With the exception of *Platycampus* and *Anoplonyx*, Rohwer's (47) Hemichroini is co-extensive. Interestingly enough, Cameron (16) considered this subfamily as forming a "connecting link" between "Selandriides" and "Nematides". Yuasa (69) claimed his larval studies confirmed Rohwer in that the grouping of *Caliroa* and *Phyllotoma* in the Hoplocampinae was invalid, despite the contentions of Konow (36) and Enslin (23) to the contrary. Yuasa examined larvae of three species in what he termed the Hoplocampinae, viz. *Marlattia* (*Anoplonyx*), *Hemichroa*, and *Caulocampus*. On the basis of the salivary glands, the last two species warrant separate grouping intermediate between the Selandriinae and the bulk of the Nematinae. On the other hand, the two species might just as well have arisen early in the nematine line as Ross' (52) arrangement suggests.

Platycampus luridiventris Fall. (Det. R.B.B.). Host, *Alnus* sp. Location, England. Fig. 66.

- A 1. Pharynx, slender; oesophagus enlarged into huge crop, extending to third thoracic or first abdominal.



Figs. 63. *Hoplocampa testudinea* (Klug). 64. *Caulocampus acericaulis* (MacGillivray). 65. *Hemichroa* (*Hemichroa*) *crocea* (Fourcroy). 66. *Platycampus luridiventris* Fallen.

2. Mid-gut, fairly stocky, short, loosely divided into three parts by means of muscular constrictions, first two-thirds surface "plushy" effect outside appearance of epithelium and muscular sheaths.
- B. Approximately twenty-one separate tubules enter gut. Five mid-ventral region, extend approximately one-eighth length of mid-gut anteriorly, coil posteriorly, two on each side extend about one-twelfth the length, then posteriorly. Remaining tubules gradually extend a greater distance anteriorly, levelling off at one-fifth the mid-gut length.
- C. Salivary glands, single pair of main, as in *Hemichroa* and *Caulocampus*, faint indication alternations in diameter along the ducts. Round salivary-gland cells.
- E. Ventral-abdominal eversible glands present.

When Ross (52) synonymized *Marlattia* with *Anoplonyx*, he mentioned that the forms had been considered subgenera of *Hemichroa* and *Platycampus* respectively, separation of the group being based upon the presence or absence of the second radial cross-vein. Further examination showed such variation within a species that the character was discarded. *Anoplonyx* was removed from *Platycampus*, however, and these two genera with *Hemichroa* hold interesting positions among the more generalized Nematini.

The salivary arrangement in *Platycampus* is, as mentioned, similar to that of *Caulocampus* and *Hemichroa* and the same conclusions apply to all (see under *Hemichroa*). The regular variability in the distance covered anteriorly by the Malpighian tubules is a modification of the "typical" nematine one, as shown by *Hemichroa*. Since the distance travelled anteriorly varies from one-fifth of the gut length to one-twelfth, it is tempting to suggest it as an intermediate condition between that of the Cladiini (one-fifth) and the typical Nematini arrangement. All that may justifiably be said, however, is that the *Platycampus* arrangement is fairly specialized.

Anoplonyx sp. Host, *Larix laricina* (Du Roi) K. Koch. Location, Ottawa, Ont., Canada. Fig. 67.

- A 1. Pharynx, narrow; oesophagus extensible into huge, thin-walled crop, stretching as far as second or third abdominal segment.
2. Mid-gut short, stocky with longitudinal markings. Histologically, rectangular-shaped cells give way to epithelium of square cells midway along gut. Posteriorly epithelial cells thinner and taller.
- B. Fourteen Malpighian tubules, separate entrance to mid-gut. Each tubule extends anteriorly approximately one-twelfth length gut, turns posteriorly, bound perirectally. Arrangement "typically nematine" except half the ordinary number of tubules. Slight indication of 2-by-2 tendency to clump in the tubules.
- C. Salivary glands, single pair of main, small pair of accessory. Two rows gland cells follow length of duct, individual attachment. Indication alternation in duct diameter.
- D. Thick fat sheath.
- E. Ventral-abdominal eversible glands present.
- F. Cuticle with peculiar surface proliferations, sculptured layer of secretion over epicuticle.

Ross (52) claims that the division of the Nematinae into two or more sub-families, obscures its definite pattern, "an almost perfectly intergraded chain of conditions ranging from the most primitive genus, *Hoplocampa*, to a closely-knit,

specialized group of genera including *Pristiphora*, *Nematus* and *Euura*". *Anoplonyx* completes the sample of four available species of generalized genera of the Nematini postulated by Ross (52) and shows intermediate salivary ducts with more traces of alternations in diameter. The Malpighian tubules, although halved in number, are, as in *Hemichroa*, nematine in arrangement.

Pristiphora erichsonii (Hartig). Host, *Larix laricina*. (Du Roi) K. Koch. Location, Ottawa, Ont., Canada. Introduced. Figs. 68, 144.

- A 1. Pharynx, narrow; oesophagus pear-shaped, globular, enlarging into fair-sized crop. Histologically, clear ovoid cells visible in flaps of oesophageal invagination.
- 2. Mid-gut stocky, divided into three regions: (1) with deep longitudinal folds; (2) transversely striate; (3) smooth. Histologically, tall, slender, epithelial cells give way to cells gradually decreasing in height posteriorly. Accompanying increase in "cilia" length noticeable. Anterior half of gut with uniform epithelial lining; posterior half thrown into series of light folds.
- B. Twenty-eight Malpighian tubules enter mid-gut, distribution and arrangement "typically nematine".
- C. Salivary glands, single pair of main, two small pairs of accessory. Ducts uniform in diameter as in Diprionidae, gland cells thickly clumped along length, clusters of two, three, or four emptying into duct.
- D. Thick fat sheath binds internal organs, no regional distribution.
- E. Ventral-abdominal eversible glands on segments 1 - 7. Glandubae found, protuberances of cuticular surface.
- F. Epicuticle, thin; exocuticle fairly thick; endocuticle thick; rounded to conical tubercles and spines protruding.

The genus *Pristiphora* and the remaining genera in the Nematini are spoken of by Ross (52) as forming the "blossom" of the nematine stem, a group of "specialized" genera fittingly described as being in "chaotic condition taxonomically". Use of accepted adult characters is insufficient and Ross states that detailed genitalic and larval characters are necessary for clarification. Ross regards *Pristiphora* as the oldest genus in the group, judging from extreme differences in the male genitalia and its possession of a "generalized" type of penis valve. *P. erichsonii* is a "typical specialized Nematine" in Malpighian tubule arrangement and salivary gland structure.

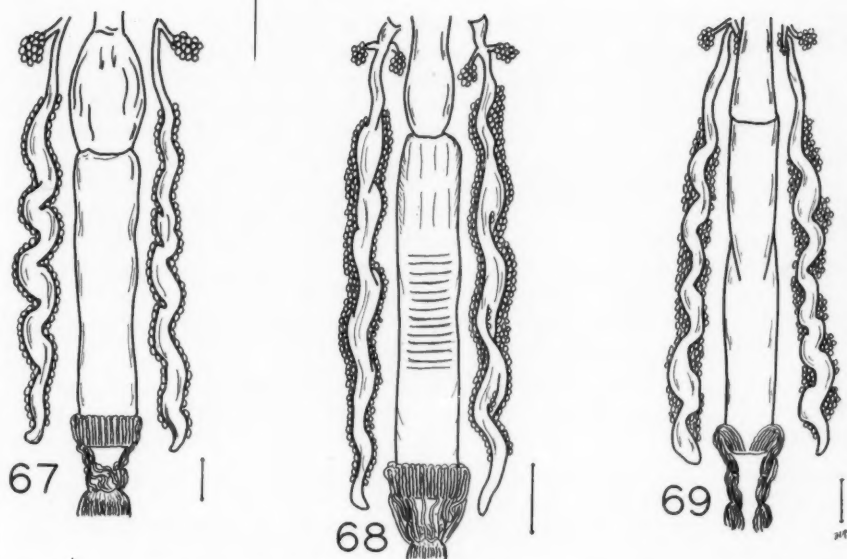
Pristiphora geniculata (Hartig). Host, *Sorbus aucuparia* (L.) Ehrh. Location, Ottawa, Ont., Canada. Fig. 69.

- A 2. Mid-gut unmodified.
- B. Malpighian tubules typical nematine arrangement, except mid-dorsal space interrupts tubule distribution, possible indication of beginnings of clumping.
- C. Salivary glands as in *P. erichsonii*, except one pair accessory ducts instead of two.
- E. Eversible glands differ in gross shape and structure; cellular body in *geniculata*, clear sheath in *erichsonii*.

On the basis of the very slight difference in Malpighian tubule arrangement, *geniculata* might be considered a more advanced form than *erichsonii*.

Pristiphora winnipeg (Norton). Host, *Picea glauca* (Moench) Voss. Location, Manitoba, Canada. Fig. 70.

- A 3. Two rows rectal teeth, one each in colon and rectum.



Figs. 67. *Anoplonyx* sp. 68. *Pristiphora erichsonii* (Hartig). 69. *Pristipobra geniculata* (Hartig).

- B. Approximately 20 Malpighian tubules arranged in typical nematine fashion.
- E. Eversible glands on abdominal segments-1 - 7, mottled grey appearance, greater resemblance to cellular body of *geniculata* than to clear sheath of *erichsonii*.

Pristiphora alnivora Hartig. (Det. R.B.B.). Host, *Aquilegia* sp. Location, England.

The anatomy of this species is so close to that of *geniculata*, even to the presence of a mid-dorsal space, that it is unnecessary to illustrate it.

Although there appear to be some distinct phylogenetic groups within the *Pristiphora*, a study on a world-wide basis is necessary to ascertain species characters. Benson (6) and Malaise (39) have undertaken studies of the distribution of members in the genus in arctic and arctic-alpine tundra.

Pikonema alaskensis (Rohwer). Host, *Picea glauca* (Moench) Voss. Location, Ottawa, Ont., Canada. Figs. 71, 145.

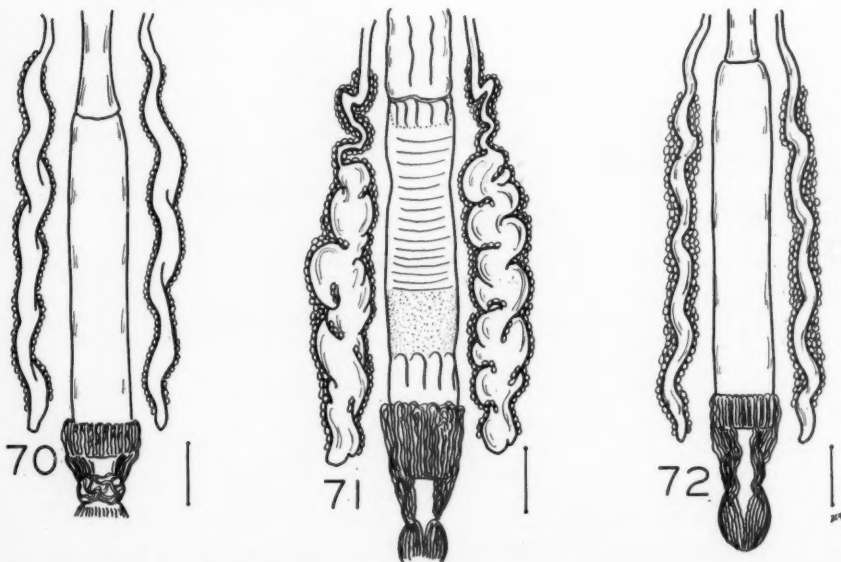
- A 1. Pharynx, narrow; oesophagus enlarged into capacious crop, externally longitudinally marked. Histological evidence of oesophageal invagination, flaps with clear ovoid cells.
- 2. Mid-gut, four regions: (1) approximately one-eighth of gut-length, narrow, tight sphincter-like band on anterior edge, followed by six deep longitudinal folds; (2) extending to approximately half length gut, transversely striate; (3) somewhat less than one-quarter length, roughly "speckled" externally, no crypt-like cells apparent; (4) slightly over one-quarter length, delimited anteriorly by deep longitudinal folds, continues smooth to hind-gut junction. Mid-gut epithelial cells show general antero-posterior transition from tall cylindrical cells to shorter cuboidal.

3. Rectum alone with single row of "rectal teeth".
- B. Approximately 28 evenly-spaced Malpighian tubules enter mid-gut. Tubules coil anteriorly approximately one-third their own length (about one-fifth length of mid-gut) turn, collected perirectally. Distribution closer to that of the Diprionidae or Cladiini than of the Nematini.
- C. Salivary glands, single pair of main, small pair of accessory. Ducts of uniform diameter. Gland cells thickly clumped in two rows along each duct, individual attachment posteriorly in small clusters anteriorly.
- D. Abdominal fat sheath thick loose accumulation of large fat cells.
- E. Ventral thoracic gland may be present. *No trace of ventral-abdominal eversible glands.* Glandulae scattered about surface.
- F. Extremely thick epicuticle, possibly extra excretion laid over epicuticle. Exocuticle and thick endocuticle also present.

Pikonema alaskensis, with its atypical Malpighian tubule arrangement, capacious crop and, above all, lack of ventral-abdominal eversible glands, occupies a peculiar position at least in the genus *Pikonema* if not in the Nematini.

Pikonema dimmockii (Cresson). Host, *Picea glauca* (Moench) Voss. Location, Ottawa, Ont., Canada. Fig. 72.

- A 1. Pharynx, narrow; oesophagus slender, pear-shaped, extensible into slight crop.
2. Mid-gut uniform, fairly stocky tube.
3. Rectum alone with single row "rectal teeth".
- B. Twenty-eight Malpighian tubules, typically nematine in distribution, extend anteriorly.
- C. Salivary glands as in *alaskensis*, salivary gland cells individually attached, in single rows along ducts.



Figs. 70. *Pristiphora winniipeg* (Norton). 71. *Pikonema alaskensis* (Rohwer). 72. *Pikonema dimmockii* (Cresson).

- D. Compact fat sheath binds salivary glands to gut.
- E. Ventral-abdominal eversible glands present on abdominal segments 1 - 7.

Ross (52) created within his Nematini the genus *Pikonema*, a compact series of spruce feeders comprising the three species, *P. ruralis*, *P. alaskensis* and *P. dimmockii*, of which only the last two have been available for anatomical comparison. While *P. dimmockii*, the type species, possesses characters that warrant its inclusion in the Nematini, *P. alaskensis* differs strikingly in its crop, divisions of the mid-gut, and arrangement of Malpighian tubules, as well as in its lack of ventral-abdominal eversible glands, the latter the only larval character consistently noted in sawfly literature as peculiar to the Nematini, Cladiini and Pseudodineurini. Adults of *dimmockii* and *alaskensis* are separable only on the basis of an obscure genitalic character and are accordingly considered congeneric. Externally the larvae are easily separable in biology and in colour, pattern, cuticular covering, glandubae, and other characters. As members of a subfamily of fairly variable larval form, however, no separation feature has been described that has seemed sufficiently valid to justify over-riding the extreme similarity of the adults.

Despite the adult similarity and the possibility that *alaskensis* might occupy an extreme position in the Nematini-Cladiini-Pseudodineurini group, the writer stresses that throughout this study, ventral-abdominal eversible glands are found only in the Cladiini, the single member examined of the Pseudodineurini, and all Nematini with the exception of *Pikonema alaskensis*.

The inclusion of *P. alaskensis* in the Nematini is anomalous, and its specific characters appear to warrant generic separation from *Pikonema*, if not the creation of a separate tribe.

Croesus latitarsus Norton. Host, *Betula*. Location, Ottawa, Ont., Canada. Fig. 73.

- A 1. Pharynx, narrow; oesophagus slender, pear-shaped, expanding into crop-like region.
- 2. Mid-gut roughly divided into three regions: (1) slightly less than half gut length, subdivided by constriction midway, transversely striate; (2) about same length, longitudinally deeply folded; (3) transversely striate.
- B. Malpighian tubules, 28; structure and arrangement, typically nematine.
- C. Salivary glands, single pair main, small pair of accessory. Ducts uniform in diameter, gland cells loosely clustered, join main ducts in groups of two.
- D. Separate fat sheaths for salivary glands and alimentary tract.
- E. Ventral-abdominal eversible glands on segments 1 - 7. Glandubae on body surface.
- F. Cuticle with small spines and spicules as well as larger spines, the latter hollow, presumably glandular in nature.

Croesus is considered to be closely related to *Nematus* and its internal anatomy stresses this similarity. It is difficult to interpret regional modification of the mid-gut as a character either more specialized or more primitive than the smooth gut of *Nematus*.

Croesus septentrionalis L. (Det. R.B.B.). Host, *Corylus*. Location, Scotland. Fig. 74.

- B. Thirty-four Malpighian tubules, typically nematine.
- E. Ventral-abdominal eversible glands on abdominal segments 1 - 7, glands twice length of abdominal prolegs, very long, almost double size found in *latitarsus*.

Croesus latipes Vill. (Det. R.B.B.). Host, *Betula* sp. Location, England.

B. Twenty-eight tubules, arranged irregularly, alternating longer distance covered anteriorly approximately one-tenth length of gut with normal nematine distance.

E. Ventral-abdominal eversible glands as those of *septentrionalis*.

Nematus (Holcocneme) coeruleocarpus Htg. (Det. R.B.B.). Host, *Salix* sp. Location, England. Fig. 75.

A 1. Pharynx and oesophagus slender, crop slight.

2. Mid-gut marked anteriorly by transverse thick fold and invagination, followed by approximately six longitudinal folds. Continues smooth to hind-gut.

B. Thirty-eight Malpighian tubules, more widely separated dorsally. Tubules extend approximately one-sixth length of gut anteriorly, as in *Pikonema alaskensis*, then coil posteriorly perirectally.

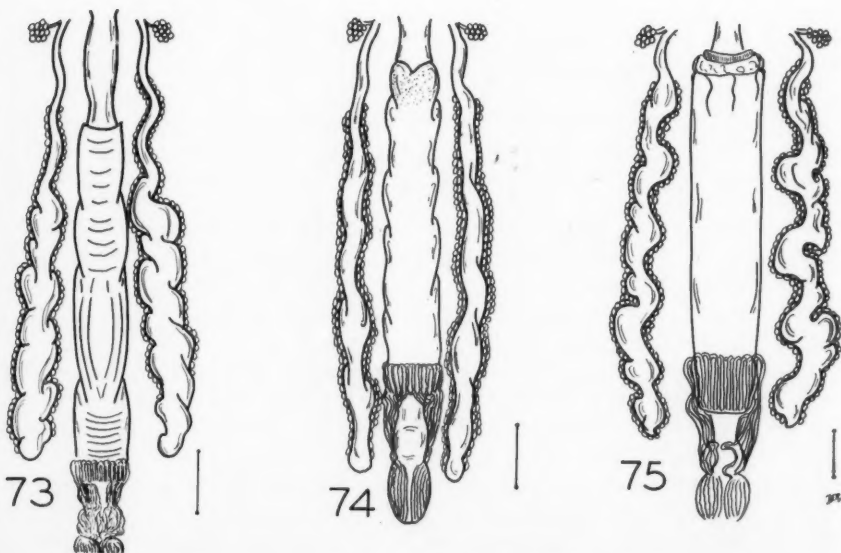
C. Salivary glands, single pair of main, two small pairs of accessory. Single row of cells down each side of uniform ducts, individually attached.

E. Ventral-abdominal eversible glands equal in length to abdominal prolegs.

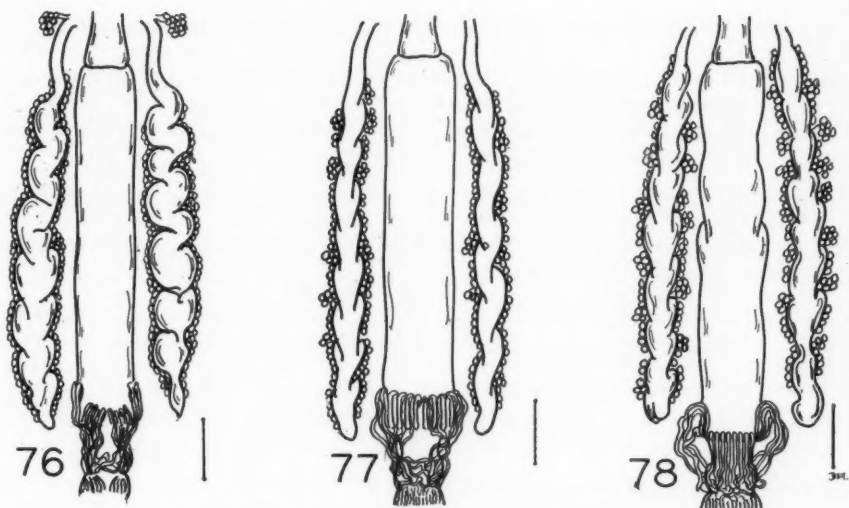
On the basis of Malpighian tubule arrangement, *coeruleocarpus* diverges somewhat from the typical nematine pattern. Other internal characters, however, suggest that it is possibly a more generalized Nematine than *Pristiphora* or *Nematus* (*Nematus*).

Nematus (Pteronidea) ventralis Say. Host, *Salix* sp. Location, Ottawa, Ont., Canada. Figs. 76, 147.

A 1. Pharynx and oesophagus narrow; no obvious crop but region probably capable of expansion.



Figs. 73. *Croesus latitarsus* Norton. 74. *Croesus septentrionalis* Linnaeus. 75. *Nematus (Holcocneme) coeruleocarpus* Hartig.



Figs. 76. *Nematus* (*Pteronidea*) *ventralis* Say. 77. *Nematus* (*Pteronidea*) *olfaciens* Benson. 78. *Nematus* (*Pteronidea*) *leucotrochus* (Hartig).

2. Mid-gut, long slender uniform tube, well marked transverse striations anteriorly.
3. Hind-gut, unmodified.
- B. Twenty-eight Malpighian tubules evenly distributed about gut, extending anteriorly about one-twelfth gut length, slight variation from typical nematine pattern in four mid-ventral tubules extending about one-fourteenth length anteriorly consistently, four on each side extending gradually greater distance anteriorly, remaining tubules, one-twelfth.
- C. Salivary glands, single pair of main, two pairs small of accessory. Gland cells cluster, join ducts in groups of two and three.
- E. Ventral-abdominal eversible glands on segments 1-7. Cask-shaped glandubae on body surface.

Nematus (*Pteronidea*) *pinguidorsum* Dyar. Host, *Betula alba*. Location, Ottawa, Ont., Canada.

Similar to *ventralis*, except mid-gut entirely smooth, single pair of accessory glands, uniform Malpighian tubule arrangement.

Nematus (*Pteronidea*) *olfaciens* Benson. (Det. R.B.B.). Host, *Ribes* sp. Location, Scotland. Fig. 77.

- A 1. Pharynx and oesophagus narrow; latter expanded into crop.
2. Mid-gut smooth.
- B. Twenty-eight evenly-spaced tubules, extending one-twelfth mid-gut length anteriorly, typically nematine except for mid-ventral space, indication of beginning of clumping.
- C. Salivary glands, single pair of main, two small pair of accessory. Four or five gland cells per clump entering ducts.
- E. Ventral-abdominal eversible glands on segments 1-7.

Nematus (Pteronidea) leucotrochus Htg. (Det. R.B.B.). Host, *Salix*, sp. Location, Scotland. Fig. 78.

- B. As in *olfaciens* except 30 Malpighian tubules, eight mid-ventral not extending anteriorly but directly posteriorly, tightly packed band of tubules, remainder extend anteriorly approximately one-twelfth length gut, turn posteriorly, bound perirectally.

Nematus (Pteronidea) melanaspis Htg. (Det. R.B.B.). Host, *Populus* sp. Location, Scotland. Fig. 79.

- B. Twenty-eight tubules, mid-dorsal gap, tubules extending one-tenth length of gut anteriorly.

Nematus (Pteronidea) pavida Lep. (Det. R.B.B.). Host, Unknown. Location, Scotland.

- B. Twenty-two tubules, wider spacing dorsally, no gap dorsally or ventrally.

Nematus (Pteronidea) spiraeae Zadd. Host, *Aruncus silvester* Kosl. Location, Scotland.

- B. Twenty-eight tubules, typically nematine. Ventral-abdominal eversible glands up to five times length abdominal prolegs.

Nematus (Pteronidea) ribesii Scop. Host, *Ribes* sp. Location, Canada, Scotland.

- B. Strikingly similar to *ventralis* with 28 Malpighian tubules. The four mid-ventral tubules extend anteriorly slightly under one-twelfth gut length, four on either side about one-twelfth, the remainder about one-tenth, or farther.

Some 30 additional species, very similar to the *Nematus (Pteronidea)* type are separable with difficulty on the basis of external larval and adult characters while appearing identical internally. Ross (52) says of *Nematus* "The genus has hitherto been considered as three or four separate ones. There seem to be no constant adult, larval, or biological differences, at least none that coincide with each other." With this in mind, he grouped *Nematus*, *Pteronidea*, and *Pontania*, as subgenera of the genus, noting there had been no attempt to establish "absolute diagnostic differences between them". He divided the subgenus *Pteronidea* into loose groupings according to food plant or general resemblance of components, e.g. *ventralis*, *aericeps*, *magus*, *mendicus*, and *ribesii* groups. There are many species listed that have not as yet been grouped as well as complexes of synonymized forms in all groups. Yuasa (69) said that *Pteronidea* is rich in number of species and, together with a few related genera, is widely separated from other Tenthredinidae by the presence of suranal caudal protuberances. He claimed that "color and coloration and the presence of setiferous tubercles and their arrangement are useful characters in separating species". As in the Diprionidae, extreme similarity in form demands accurate mass rearings to establish the validity of such characters as body colour and setal pattern in setting species and genus limits, and in determining anatomical variation, e.g. Malpighian tubule and ventral-abdominal eversible glands as correlative clues towards separation. The genus is unquestionably highly and, moreover, recently evolved, judging from the complexity and overlap so evident in the "species".

Nematus (Pontania) sp. Host, *Salix* sp. Location, Ottawa, Ont., Canada. Fig. 80.

- A 1. Pharynx and oesophagus narrow.
2. Mid-gut fairly straight tube.
B. Eight separate tubules. Nematine in distribution. All bound perirectally.

- C. Salivary glands, single pair of main, no pair of accessory apparent, probably minute.
- E. Ventral-abdominal eversible glands on segments 1-7.

Pontania is easily recognizable as a typical Nematine despite the reduction in tubule number, which might be either a secondary modification or an indication of relatively primitive position within the more specialized Nematini. In view of its specialized gall-forming habit, possibly the former theory is the more tenable. Ross (52) mentioned that, when venation was the sole criterion for separation, the species included in the subgenus *Pontania* were often confused with those of *Euura*. Larvae of *Euura* sp., provided by W. Y. Watson of the Forest Insect Laboratory, Sault Ste. Marie, were inseparable, internally, from those of *Pontania*.

Amauronematus humeralis Lep. (Det. R.B.B.). Host, *Salix* sp. Location, England. Fig. 81.

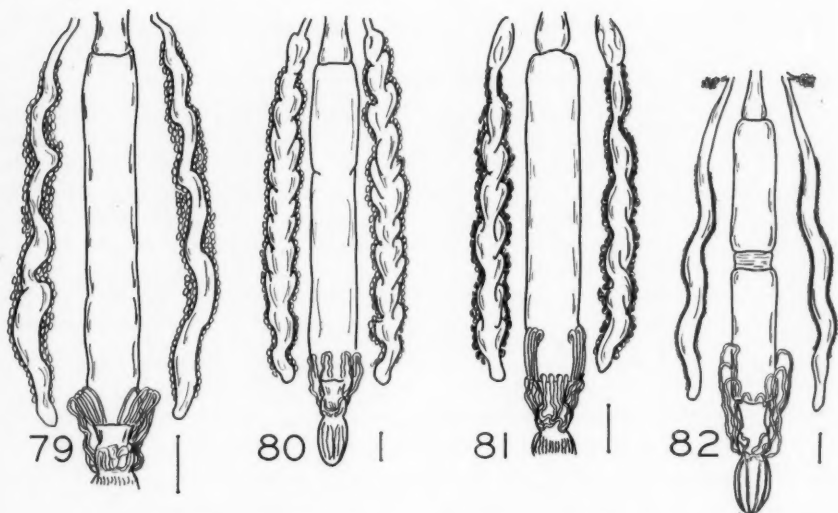
- A 1. Pharynx and oesophagus, slender; no crop.
- 2. Mid-gut uniform.
- B. Twenty-two tubules, five ventral extend directly posteriorly, band formation, (see *Pteronidea leucotrochus* for somewhat similar formation). Remainder extend anteriorly approximately one-sixth gut-length as in *Pikonema alaskensis* and *Nematus (Holcocneme)*.
- C. Salivary glands, single pair of main, two small pairs accessory.
- E. Minute ventral-abdominal eversible glands.

Nematus (Nematus) abbottii (Kirby). Host, *Robinia pseudoacacia* L. Location, Ottawa, Ont., Canada.

A green larval form, tentatively identified as *Nematus (Nematus) abbottii*, has typically nematine Malpighian tubules.

As seen, the anatomy of the four species of generalized Nematini, often grouped as the Hemichroini, reveals at least two characters suggesting a primitive arrangement; the indication of alternation in diameter in the salivary ducts and some variation from the expected "typical Nematine" number and arrangement. Differences are found in the number of pairs of accessory salivary glands, but the main ducts of all other Nematini examined were uniform. *Nematus (Nematus) abbottii*, *Nematus (Pteronidea) olfaciens*, *N. (P.) spiraeae*, all unidentified species of "*Pteronidea*", *Croesus latitarsus*, *Pikonema dimmockii*, and the genus *Pristiphora* show the typical nematine pattern. *Nematus (Pteronidea) ventralis*, *N. (P.) pinguidorsum*, *N. (P.) ribesii*, and *Croesus latipes* have 28 tubules, but differ in arrangement and extent traversed anteriorly. *Croesus latitarsus* and *C. septentrionalis* have 34 typically arranged tubules. In *Pikonema alaskensis*, with 28 tubules, and *Nematus (Holcocneme)* with 34, the tubules extend anteriorly about one-sixth the gut-length. *Nematus (Pteronidea) leucotrochus* and *Amauronematus* differ in number, 30 and 22 respectively, and in a band of tubules extending directly posteriorly in the mid-ventral region. *Nematus (Pontania)* has 8 tubules, nematine in arrangement.

This summary indicates that internal anatomy, although of use in suggesting trends in the Nematini, cannot be expected to produce any clear indication of group segregation or even accurate species separation. A more intensive study of the ventral-abdominal eversible glands and the Malpighian tubule arrangement may reveal more direct separation points.



Figs. 79. *Nematus (Pteronidea) melanaspis* Hartig. 80. *Nematus (Pontania)* sp. 81. *Amauronematus humeralis* Lepeletier. 82. *Kerita fidala* Ross.

Tribe Pseudodineurini

Kerita fidala ROSE. (Det. H.H.R.). Host, *Mertensia virginica* (L). Location, Illinois, United States. Fig. 82.

- A. 1. Pharynx, narrow; oesophagus enlarged into slight crop.
- 2. Mid-gut smooth, unmodified to point mid-way to hind gut, here constricted region for one-twelfth gut length. Remainder of gut smooth.
- B. Malpighian tubules, nine, separate entrances to gut, at evenly-spaced intervals. Tubules extending variable distance anteriorly, coiling posteriorly, bound perirectally. The two mid-ventral tubules extend very slightly anteriorly.
- C. Salivary glands, single set of main, small pair of accessory. Ducts uniformly expanded, bordered by rows of small round gland cells.
- E. Ventral abdominal eversible glands present.

In 1937, Ross (52) included his new genus *Kerita* among the more generalized of the Nematinae, saying, "This genus represents, with *Pseudodineura*, the end of a small, specialized branch of the Nematinae. The progenitors of this group were probably forms allied to *Hemichroa*. The genus *Kerita* resembles only *Pseudodineura* from which it differs in the smaller and more compact ocellar triangle, the distinct malar space and the larger teeth on the mandibles." It is of interest that in his latest revision (53), *Pseudodineura* and *Kerita* are granted tribal status, one of the four tribes comprising the Nematinae.

On external anatomical grounds, *Kerita* possesses no outstanding character tending to separate it from the species in the other two tribes examined; internally, it possesses an unusual waist-like modification of the mid-gut. The low tubule number of nine and irregular distribution suggest a primitive position of the species within its tribe and within the Nematinae as well.

Subfamily Athaliinae. (Athaliini of the Blennocampinae (Benson))

Benson's (4) Athaliini, which he included in the Emphytinae (Allantinae) and incorporated as a tribe in the large Blennocampinae in his latest revision (8), contains the single genus *Athalia* represented by some Palearctic, Ethiopian, and Oriental species unknown or unrecorded in the New World. Benson mentioned that the group probably merits subfamily rank (4). Its incorporation as a subfamily in this work is a matter of convenience since arrangement of the *Athalia* group as a tribe in Benson's Blennocampinae would at this point involve a premature discussion of one of the writer's major hypotheses.

Athalia rosae (L.). (Det. R.B.B.). Host, *Brassica campestris* L. Location, England. Fig. 83.

- A 1. Pharynx and oesophagus slender, latter expandible into slight crop.
- 2. Mid-gut, stout long uniformly "plushy" surface from protruding muscle and epithelial cells, no crypt-like protuberance effect.
- 3. Hind-gut unmodified.
- B. Ten Malpighian tubules enter mid-gut, six ventrally extending anteriorly, four dorsally extending posteriorly.
- C. Salivary glands, single pair, ducts expanded anteriorly into large somewhat irregularly shaped reservoirs, continue posteriorly, fairly narrow tubes, squared discontinuous appearance. At regular intervals, apparent indication of alternate bulb-like expansions and narrow junctions only very little secretion in ducts of available *rosae* larvae which were all in collapsed state and distorted. Gland cells, hexagonally-shaped, entering main ducts by fairly elongate secondary ducts in twos and threes.
- F. Cuticle, "bubbly" appearance from epicuticle, and, in all probability an extra layer of secretion raised in a series of minute lobe-like projections.

Athalia himantopus Klug. (Det. R.B.B.). Host, *Brassica oleracea* L. Location, Southern Rhodesia. Fig. 84.

- A 1. Pharynx, slender; oesophagus expanding into small crop.
- 2. Mid-gut stocky, fairly long, surface "plushy" in appearance from microscopic protruding cells not so distinct as single-cell crypts of the Cimbicidae but producing soft villi-like covering on gut, faint trace of underlying epithelial outline in mosaic effect.
- B. Ten tubules, six ventral extending anteriorly in three lots of two tubules, four dorsal extending posteriorly.
- C. Salivary glands, single pair. Slender duct opens into rectangularly-shaped reservoir, continues posteriorly in a series of alternate bulb-like expansions, and narrow connection portions almost as long as bulbs. Gland cells in clusters of 2-6, pear-shaped to hexagonal, empty into duct by small fairly long secondary ducts.
- F. Cuticle "bubbly".

Athalia sp. 1. (Det. R.B.B.). Host, "Water Cress". Location, South Africa. Fig. 85.

- A 1. Pharynx and oesophagus slender. Possible crop-like expansion.
- 2. Mid-gut, first one-fifth characterized by three deep transverse folds. "Plushy" appearance to surface.
- B. Ten tubules, evenly-spaced, six ventral, anteriorly directed, four dorsal, posteriorly. Tubules appear to enter common expanded hollow ring circling gut at junction of mid- and hind-gut, collecting duct. Posterior tubules first circle latero-ventrally.

- C. Salivary glands, single pair, long rectangular reservoirs extending to approximately end of third thoracic. Remainder of duct slender in collapsed state, indications of bulb-like expansions and narrow junctions as in previous forms. Gland cells large, pear-shaped to hexagonal, entering duct by small, fairly long side branches, branching off main duct fairly evenly in twos.

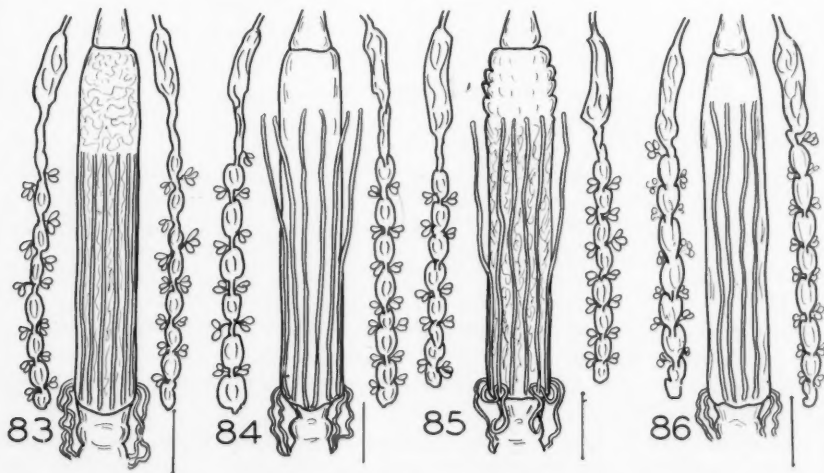
- F. Cuticle "bubbly".

Adults reared from sp. 1 larvae key in Benson to "close to *Athalia cordata* Lep." but saw not entirely according to given description.

Athalia liberta (Klug). (Det. R.B.B.). Host, *Cardamine hirsuta* L. Location, England. Fig. 86.

- A 1. Pharynx and oesophagus slender; indication of crop.
2. Fairly smooth mid-gut.
- B. Ten tubules, four ventral, two on each side of mid-ventral line, two on each side laterodorsally, and two posteriorly, one on each side mid-dorsal line.
- C. Salivary glands, single pair, slender ducts enlarge into long round to rectangular reservoirs; from reservoirs ducts narrow and expand alternately to end. Bulb-like expansions taper gradually into each other as opposed to the well-defined limits of bulb and junction in other species. Resemblance to duct arrangement in Selandriinae not marked. Large hexagonal gland cells enter main duct by small fairly long secondary ducts, two to six per cluster. Branch ducts off from narrower portions of main ducts.
- F. Cuticle "bubbly".

Benson (7) states that the larvae of *liberta*, once included in a "*rosae* complex", have not been distinguished externally from those of *rosae*. Separation is on the basis of minor differences and host preference.

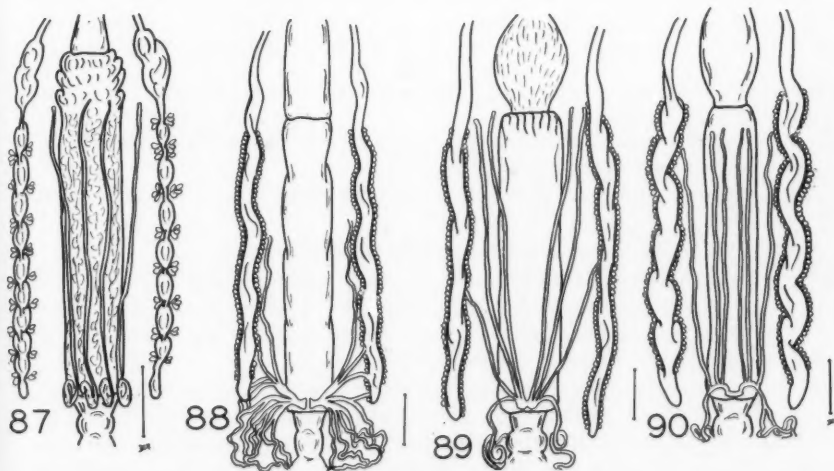


Figs. 83. *Athalia rosae* (Linnaeus). 84. *Athalia bimantopus* Klug. 85. *Athalia* sp. 1.
86. *Athalia liberta* (Klug).

Athalia sp. 2. (Det. R.B.B.). Host, "Horse Radish". Location, South Africa. Fig. 87.

- A. 2. Mid-gut, first half angularly striate, typhlosole-like effect longitudinally, three raised transverse folds carried along to junction with hind-gut.
- B. Nine tubules. Six ventral tubules extend initially anteriorly, loop posteriorly and return anteriorly floating freely in the body cavity, first loop greatly swollen beyond width of anterior extension of each tubule. Dorsally one tubule enters mid-dorsal line, one tubule on either side, all extending posteriorly, bound perirectally.
- C. Salivary glands, single pair, large rectangular reservoir, alternate bulb-like expansions down slender duct, close to *liberta* in general appearance. Large hexagonal gland cells enter ducts by fairly long branch ducts, entering between bulb-like expansions. Clusters of four or five cells.
- F. Cuticle "bubbly".

Benson (8) characterizes the larvae of the Athaliini as "mostly velvety bluish-black or grey, often unicolorous", antennae of adults more than 9-segmented, mesopleural suture strongly sinuate and hind margin of mesepisternum emarginate above and upper part of the mesepimeron rounded and convex. Externally many of the species of *Athalia* have proved difficult, if not impossible, to separate in the larval stage. Forms not distinguished from *A. rosae* are *A. lugens*, and *A. lineolata*, as well as *liberta*. Host records and adult studies have provided sole criteria for separation. Their anatomy stresses the resemblance between the Athaliini and the Selandriinae in salivary-gland structure, the reservoir, alternate expansions along the duct, and method of junction of the gland cells. The bulb-like expansions found in the Athaliini are rounded, with wide fairly indistinct junctions, resembling the pattern found in the *Dolerus* group. The gland cells in the Athaliini are distinctive in themselves, with their pear- to-hexagonal shape. The foregoing characteristics indicate a fairly primitive salivary gland structure, pointing to an extremely close relationship with the



Figs. 87. *Athalia* sp. 2. 88. *Empria* (*Parataxomus*) *multicolor* (Norton). 89. *Monostegia abdominalis* (Fabricius). 90. *Ametastegia* (*Ametastegia*) *equiseti* (Fallen).

Selandriinae, if not to the inclusion of the two groups in the same complex. The Malpighian tubule structure is almost identical with that of the *Dolerus* species and emphasizes an almost incredibly close parallel evolution. It appears judicious to defer conclusions based on internal anatomy until the Allantinae and Blennocampinae have been examined.

Subfamily Allantinae

Tribe Allantini

(A. Tribe Empriini of Benson)

Empria (Parataxonus) multicolor (Norton). (Det. H.H.R.). Host, *Betula* sp. Location, Ottawa, Ont., Canada. Fig. 88.

- A 1. Pharynx, narrow; oesophagus slightly conical, expandable into large crop extending to second or third thoracic.
- 2. Mid-gut long fairly wide tube, bending anteriorly near junction with hind-gut.
- 3. Ileum, large; colon, globular; rectum convoluted.
- B. Two common Malpighian stalks enter mid-gut, main axis of each at right angles to mid-ventral line, stalks directed latero-dorsally. Each stalk fans out into two large tubules, each dividing in turn into tubules directed some anteriorly, some posteriorly. Some of the latter are bound perirectally.
- C. Salivary glands single pair ducts uniform in diameter, two rows gland cells, flattened cuboidal down each side, clusters of two enter duct.
- E. Glandubae on body surface.

The subgenus *Parataxonus* of the genus *Empria* was once a genus in its own right. Adults of *E. (Parataxonus)* differ from those of *E. (Empria)* in such obscure characters as shape of angular lobes of clypeus, presence or absence of median keel, and presence of peripheral vein around hind wing in male. The structure of the salivary ducts suggests the advanced uniformly broad ducts of the Diprionidae or most of the Nematini, while the flattened cuboidal cell type is possibly an indication of a fairly generalized condition. The Malpighian tubule arrangement, about the level reached in the Cimbicidae, is in keeping with a trend to a more specialized condition of clumping.

Monostegia abdominalis (Fab.), Host, *Lysimachia* sp. Location, Ottawa, Ont., Canada, and England. Fig. 89.

- A 1. Pharynx, narrow; oesophagus expanded into huge crop, extending to first abdominal segment, thin-walled.
- 2. Mid-gut delimited anteriorly by approximately 12 deep longitudinal folds.
- 3. Ileum, colon large, scarcely delimited; rectum, huge.
- B. Two wide, common stalks fuse just before entering mid-gut. Main axis of each at right angles to mid-ventral line. Each stalk branches, sending off three anterior tubules and one lateral, which turns posteriorly and floats freely in the rectal body cavity.
- C. Salivary glands, single pair, unmodified, uniformly wide duct, single row of fairly round, large gland cells, entrance to duct individual.

Ross (52) says that *Monostegia* is closely related to *Empria* and that many workers, Enslin included, consider it another subgenus of *Empria*. Its anatomy is strikingly similar to that of *Empria (Parataxonus)*, except that the Malpighian arrangement is more reduced.



Figs. 91
H

Ametastegia (Ametastegia) equiseti (Fallen). (Det. R.B.B.). Host, *Chenopodium* sp. Location, England. Fig. 90.

- A 1. Crop as in *Monostegia*.
- 2. Mid-gut smooth.
- B. Entrance of strap-like Malpighian tubule stalk at right angles to mid-ventral line. Each wing of narrow Malpighian stalk extends anteriorly and laterally giving rise to three anterior branches and then continues posteriorly floating freely in rectal body cavity.
- C. Salivaries generally similar to *Monostegia*.

Ametastegia (Protemphytus) perla (Klug). (Det. R.B.B.). Host, *Alchemilla vulgaris* L. Location, England. Fig. 91.

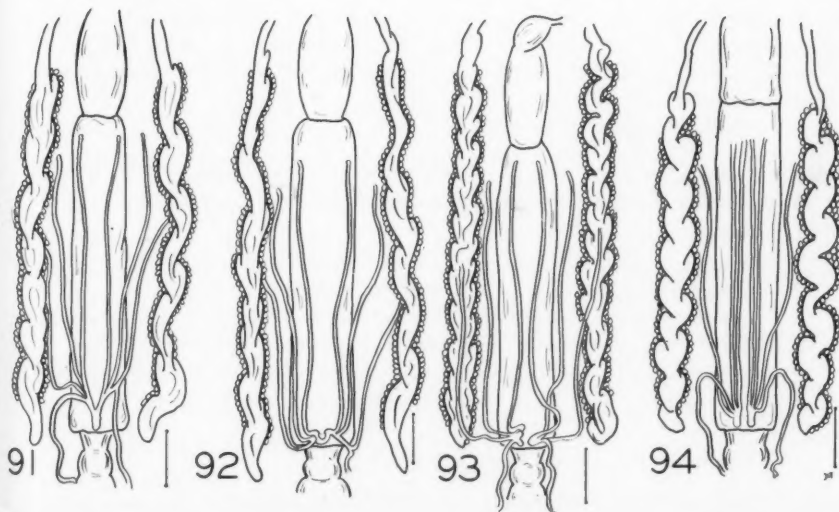
- A As in *Monostegia* and *A. (A.) equiseti*.
- B. Single common stalk to Malpighian tubules, two main branches extend anteriorly, parallel to mid-ventral line, each giving rise to three anterior and one posterior tubule.

Ametastegia (Protemphytus) carpini (Hartig). (Det. R.B.B.). Host, *Geranium* sp. Location, England. Fig. 92.

- B. Single common stalk wider than in preceding two species. Two anterior tubules given off on each side; third anterior and one posterior off together, almost constricted from main stalk.

Ametastegia (Protemphytus) pallipes (Spinola). (Det. R.B.B.). Host, *Viola* sp. Location, England. Fig. 93.

- A 1. Pharynx slender, oesophagus bulb-like, expanded into large crop extending as far as second or third abdominal segment, equal in length to half mid-gut.
- 2. Mid-gut short slender.



Figs. 91. *Ametastegia (Protemphytus) perla* (Klug). 92. *Ametastegia (Protemphytus) carpini* Hartig. 93. *Ametastegia (Protemphytus) pallipes* (Spinola). 94. *Ametastegia* sp.

- B. Two separate Malpighian stalks enter gut at approximately 20° angle with mid-ventral line. Four branches given off from each, three anterior, one posterior, latter bound loosely to rectum.
- C. Salivary glands, single pair, no trace of reservoirs; peculiar squaring of duct of salivary, suggests alternate arrangement with squared expansions, as in *Selandria* spp., however, duct is of uniform diameter. Large, rounded gland cells attached in small clusters.

Ametastegia sp. (Det. R.B.B.). Host, *Spiraea* sp. Location, England. Fig. 94.

- B. Two separate common stalks enter mid-gut; parallel to mid-ventral line, each dividing into three anterior and one posterior branch.

Ross (52) claims that *Empria* represents, in all probability, the most generalized member of his Allantinae. He groups the genera into three tribes: (1) the Allantini with a series of genera from *Empria*, through *Monostegia*, *Mono-soma*, *Aphilodactylum*, and *Allantus*, to the most specialized, *Macremphytus* and *Taxonus*; (2) the Phrontosomini with one nearctic genus, relatively generalized apart from two specialized characters; (3) the Eriocampini, with *Pseudosiobla*, *Eriocampa*, and *Dimorphopteryx*. Benson (8) gives tribal status to 5 genera in the more generalized portion of Ross' Allantini, *Harpiphorus*, *Monostegia*, *Mono-soma*, *Empria*, and *Ametastegia*.

Interestingly enough, the subgenus *E.* (*Parataxonus*), as part of the more generalized *Empria*, has the flattened cuboidal salivary gland cell type, of the more primitive subfamilies such as the *Selandriinae*. The ducts themselves, however, are uniform in diameter. The Malpighian tubule arrangement is more complex than that found in the remainder of the "Empriini". A "3 by 1" arrangement, (three anterior and one posterior) is typical of *Monostegia*. *A. (A.) equiseti* is similar except that the common stalk is strap-like. *A. (P.) perla* possesses a long, slender, common stalk. In *A. (P.) carpini*, the strap-like duct of *equiseti* is apparent and the third anterior and single posterior tubules are narrowly constricted at their attachment to the main stalks. *A. (P.) pallipes* and *Ametastegia* sp. have two main stalks entering the gut. The branching arrangement of each stalk is 3 by 1 and in addition a close approximation to that of *Allantus*. Anatomical detail is entirely in agreement with the concept of an "Empriini"-trend.

(B. Tribe Allantini of Benson)

Allantus cinctus (L.). Host, *Rosa* sp. Location, Ottawa, Ont., Canada. Fig. 95.

- A 1. Pharynx, narrow; oesophagus enlarging into fairly stout crop.
- 2. Mid-gut stocky, long.
- B. Two large separate tubule stalks enter mid-ventral line of mid-gut, axes parallel to each other. Each stalk branches into three anterior, four posterior tubules (sometimes three only on left). Posterior ones loosely bound rectally, anterior float freely.
- C. Salivary glands, single pair, ducts expansible, uniform in diameter, gland cells rounded, flank ducts in single row on each side of duct, individually attached.
- E. Glandulae evident on body surface.

Allantus calceatus (Klug). (Det. R.B.B.). Host, *Alchemilla vulgaris* L. Location, England. Fig. 96.

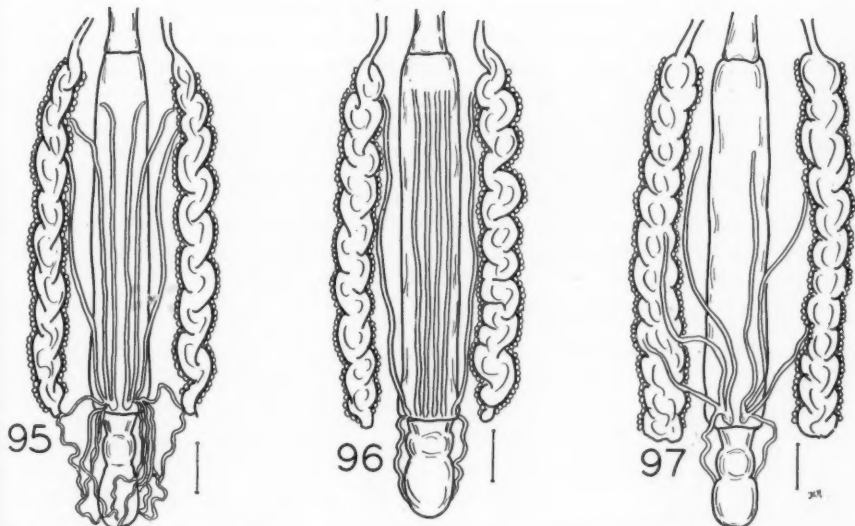
- A 1. As in *A. cinctus*.

- B. Eight separate tubules, four ventral evenly-spaced, two latero-ventral, extending anteriorly; two lateral extending posteriorly. Similar to the "3 by 1" Empriini arrangement except tubules enter gut separately.
- C. Salivary glands, single pair, uniformly wide, lightly folded; round gland cells, join duct in clusters of two or three.

Apethymus braccatus (Gmelin). (Det. R.B.B.). Host, *Quercus* sp. Location, England. Fig. 97.

Strikingly similar in detail to *A. calceatus* except:

- B. Two common stalks of Malpighian tubules inserted as in *A. (A.) pallipes*, axes at 20° angle with mid-ventral line. Four branches from each stalk, three anterior, one posterior.
- C. Salivary glands as in *A. calceatus*, thick covering of gland cells, clusters up to four and five.



Figs. 95. *Allantus cinctus* (Linnaeus). 96. *Allantus calceatus* (Klug). 97. *Apethymus braccatus* (Gmelin).

Macremphytus sp. 1. Host, *Cornus* sp. Location, Ottawa, Ont., Canada. Fig. 98.

- A 1. Pharynx, narrow; oesophagus slightly conical, extensible into broad crop stretching to first or second abdominal segment.
- B. Two wide, common stalks of Malpighian tubules directed slightly dorsally as well as posteriorly, each divides into three or four large, swollen tubules close to entrance to gut, typically four branches to left, three to right. Each swollen tubule subdivides into smaller tubules approximately three extending anteriorly, floating freely in the body cavity, remainder posteriorly loosely bound perirectally.
- C. Salivary glands, single pair of main glands, two or more small pairs of accessory. Two single rows gland cells individually attached to each duct. No trace expansions, duct uniform.

- E. Many glandubae on body surface. Wax glands (epidermal) over body. Scaly bloom secreted.

Macremphytus sp. 2. Host, *Cornus* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 99.

Answers general description of *Macremphytus tarsatus* Say on basis of larval head capsule (larvae yellow with black pattern).

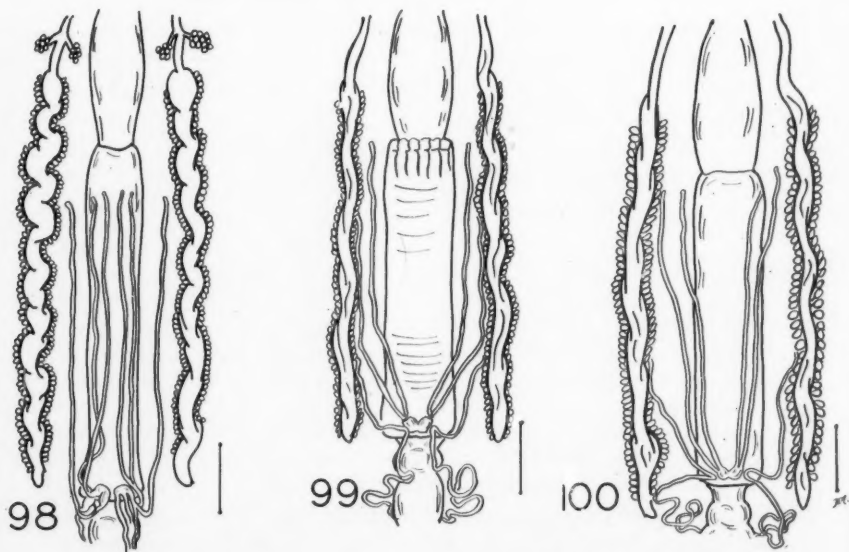
- A 1. Crop extremely large.
 2. Mid-gut delimited anteriorly by approximately 12 deep longitudinal folds thrown into transverse striations as well, general appearance series of separate glandular regions anteriorly. Heavily transversely striate to junction with hind-gut. Fairly "fuzzy" surface appearance as in *Athalia* spp.
 B. Two tubule stalks fuse at entrance to gut. At the apex two anterior branches constricted at junction. Laterally, two additional tubules, one anteriorly, and one posteriorly, these may open into fused stalk or empty directly into gut, a further indication of a "3 by 1" Emprini arrangement.
 C. Salivary glands single pair of main; ducts with a trace of squared effect, as in *Macremphytus* sp. 1. Gland cells squared as well.

Externally *Macremphytus* spp. 1 and 2 are very close. *Macremphytus* sp. 2 is closer to *Ametastegia*, *Monostegia*, and *Allantus calceatus* than to *Macremphytus* sp. 1 or to *Allantus cinctus* on the basis of Malpighian tubules.

Macremphytus sp. 3. Host, *Cornus* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 100.

Very similar to *Macremphytus* sp. 2, except no black pattern in any larval instar. Head capsule of larva similar to that of *Macremphytus* sp. 1.

- A 1. Crop extremely large.
 2. Mid-gut shiny to smooth, unstriate.



Figs. 98. *Macremphytus* sp. 1. 99. *Macremphytus* sp. 2. 100. *Macremphytus* sp. 3.

- B. Two common stalks of Malpighian tubules strikingly similar in arrangement to those of *Macremphytus* sp. 2, fuse at entrance to gut. No constrictions evident at junction of four branches on each side and at main stalks.
- C. Salivary glands as in *Macremphytus* sp. 2 but with squared ducts and large squared salivary gland cells.

Macremphytus sp. 4. Host, *Viburnum* sp. Location, Ottawa, Ont., Canada. Fig. 101.

Although Ross (53) states that "all reared species of this genus (*Macremphytus*) feed on *Cornus* spp. of the osier dogwood group", the larvae found feeding on *Viburnum* are very similar to the three *Macremphytus* spp. just described, and answer the generic requirements of *Macremphytus* alone in Yuasa's (69) key.

- A 1. Crop extremely large.
- 2. Mid-gut unmodified, fairly long and stocky.
- B. Two main stalks enter mid-ventral line separately at approximately 45° angle. Two anterior and one posterior tubule off each stalk. Striking similarity, except for number of tubules, to *Ametastegia* (A.) *pallipes* and *Apethymus braccatus*.
- C. Salivary glands single pair of main, small pair of accessory branching off main. Trace of reservoir. Suggestion of squaring in duct although uniform in diameter. Large rounded gland cells, clusters of two or three entering duct. The trend to the supposedly specialized *Macremphytus* from an intermediate in the Allantinae, e.g. *Allantus*, as suggested by Ross (52) is none too distinct anatomically. *Macremphytus* sp. 1 shows, in its unusual accumulation of posteriorly directed main stalks, an indication of specialization in tubules. The other *Macremphytus* spp. however, are close to *Allantus cinctus* which has a slight increase in number of tubules. Oddly enough internal anatomy shows just as much interspecific variation within *Macremphytus* and *Allantus* as between those genera and *Ametastegia*.

Tribe Eriocampini (Ross and Benson)

Eriocampa ovata (L.). Host, *Alnus* sp. Location, Ottawa, Ont., Canada. Fig. 102.

- A 1. Crop extremely large.
- 2. Mid-gut delimited anteriorly by five deep transverse folds each secondarily folded. Remainder of gut unmodified except last quarter, transversely striate. Surface "fuzzy" from protruding muscle and epithelial cells.
- B. Two stalks of tubules fuse at entrance to gut. Anterior ends of wing-like stalks branch into three tubules. Five tubules from sides of stalks, first and sometimes second directed anteriorly, last three or four laterally and posteriorly and loosely bound perirectally. Although pattern constant in over twenty-five specimens, two aberrants found, one with an extra set of anterior branches, the other with a single tubule entering the base of the stalk.
- C. Salivary glands, single set main, unmodified, large clumps of large, round, gland cells (approximately half diameter of duct).

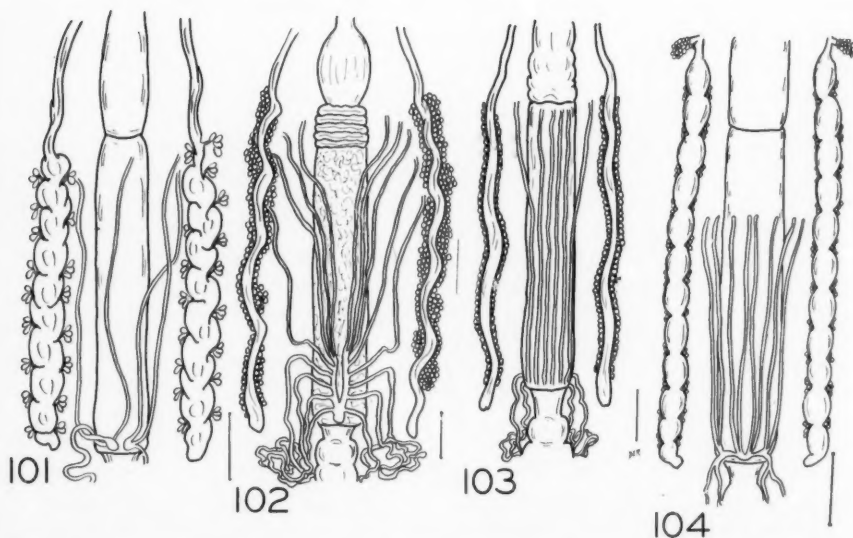
Dimorphopteryx pinguis (Norton). Host, *Betula papyrifera* Marsh. Location, Ottawa, Ont., Canada. Fig. 103.

- A 1. Pharynx, narrow; oesophagus enlarged into pronounced crop.
- 2. Mid-gut fairly stocky extends uniformly to junction with hind-gut.

- B. Ten tubules, six separate, ventral tubules extend anteriorly float freely in the body cavity; four fusing mid-dorsally, two laterals of which extend ventrally around the gut, then turn posteriorly and float freely in rectal body cavity.
- C. Salivary glands, single set of main, small pair of accessory. Each main duct unmodified, uniform in diameter flanked by two single rows of flat to cuboidal gland cells, individually attached.
- E. Many large conical tubercles projecting on body surface, glandular in nature.
(See Yuasa (69) for prothoracic eversible glands).
- F. Body surface marked by prominent tubercles, larval cuticle "bubbly" and vacuolated in appearance.

Pseudosiobla excavata (Norton). (Det. H.H.R.). Host, *Cephalanthus* sp. Location, United States. Fig. 104.

- A 1. Pharynx, narrow; oesophagus enlarged into huge crop.
- 2. Mid-gut stocky, long, extending uniformly to junction with hind-gut.
- B. Malpighian tubules, two main rectangular stalks fuse just before entrance to gut, main axes at approximately 45° angle to mid-ventral line. Each stalk branches first into two tubules directed anteriorly, parallel and close to the mid-ventral line; then laterally into two branches, the anterior of which divides into two anteriorly directed tubules and posterior of which subdivides into two posteriorly directed tubules.
- C. Salivary glands, single pair of main, small pair of accessory. No trace of reservoirs. Duct a series of alternate bulb-like expansions and narrow junctions. Salivary gland cells small, round, individually attached.



Figs. 101. *Macremphytus* sp. 4. 102. *Eriocampa ovata* (Linnaeus). 103. *Dimorphopteryx pinguis* (Norton). 104. *Pseudosiobla excavata* (Norton).

The Malpighian arrangement of *Pseudosiobla* is generally similar to that of *Ametastegia* (*Ametastegia*) *equiseti* and *Ametastegia* (*Protomphytus*) *carpini* but bears in addition a striking resemblance to the tubule pattern of certain Blennocampinae, among them *Blennocampa pusilla* and *Rhadinoceraea micans*.

In the formation of the Eriocampini, Ross (52) mentioned that the three genera involved were grouped on the basis of their rugose mesopleurae and differed radically in mandibular and antennal structure and genitalia. Praeputial genitalic lobes resemble to a certain extent those of *Empria*, and Ross suggested that the genera in question, *Pseudosiobla*, *Eriocampa*, and *Dimorphopteryx*, are "aberrant offshoots of an early stem". This is an interesting hypothesis in view of facts already mentioned and those stressed by Yuasa. The Selandriinae and Emphytinae (Allantinae) have always been considered extremely close.

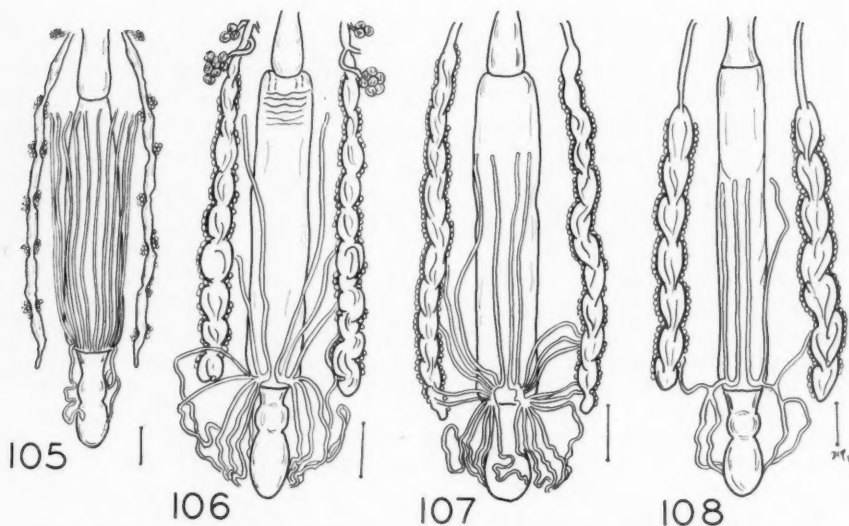
The only variations from a broad, expansible, uniform salivary duct in the Allantinae were found in *Ametastegia* (*Ametastegia*) *pallipes*, the *Ametastegia* on *Spiraea*, and *Macremphytus* spp. 2, 3, and 4. In all cases, although duct diameter is uniform, a trace of squaring is found at regular intervals along its length. Salivary gland cells are of the "primitive" flat-to-cuboidal shape in *E. (Parataxonus)*, *Dimorphopteryx*, and *Macremphytus* spp. 2 and 3. If the squared effect is any indication of a condition similar to that of the alternation of junctions and bulb-like expansions in some of the Selandriinae, it constitutes further evidence of the close relationship of the two groups. The Malpighian tubules show variations in either a "two-stalk" or a "fused-stalk", "3 by 1" branching arrangement of tubules, in confirmation of Ross' suggested trend from the "Empriini" to *Macremphytus*. The species show changes from the two-stalked, almost laterally directed, many-branching tubule arrangement of *E. (Parataxonus)*, through the "fused-stalk" condition of *Monostegia* with the "3 by 1" branching, to the separate-stalk entrancees in *A. (P.) pallipes*. *Allantus cinctus* has the large two-stalked arrangement with more than the "3 by 1" number of branch-tubules, while *Allantus calceatus* has an 8-tubule number with an independent entrance of each tubule into the gut. The final stage is the pronounced argid-like posteriorly extending stalks in *Macremphytus* sp. 1. *Eriocampa*, with its wing-like extensions of a 2-fused-stalk arrangement and the "primitive" Malpighian arrangement of *Allantus calceatus* and *Dimorphopteryx*, provide three unusual cases, the first a specialized modification, the last two a Selandriinae change, or one of the "xyelid type". It is noteworthy that *Pseudosiobla* with its increase in tubule number over the typical Empriini arrangement, represents a Malpighian formation similar to both the Empriini and the Blennocampinae.

Subfamily Blennocampinae

Tribe *Lycaotini*. (Benson's Blennocampini of the Blennocampinae).

Lycaoto sp., prob. *sodalis* (Cresson) (Det. H.H.R.) Host, *Symphoricarpos racemosus* Michx. Location, British Columbia, Canada. Fig. 105.

- A. 1. Pharynx, narrow; oesophagus, bulbous, expanding into fairly large crop.
2. Mid-gut, uniformly thick tube.
- B. Malpighian tubules, 12. Ten ventral, anteriorly extending, free-floating; two latero-ventral, coiling posteriorly, loosely attached perirectally.
- C. Salivary glands, single set of main, one of accessory. Slight indication of reservoir. Main duct extends as narrow tube, indication of alternation in diameter. Two or three gland cells per cluster, enter duct in rows along length.



Figs. 105. *Lycaota* sp. 106. *Tomostethus multicinctus* (Beauvois). 107. *Tomostethus nigrinus* (Fabricius). 108. *Pareophora minuta* (MacGillivray).

The Lycaotinae were placed by Konow (36) in his Selandriades, a group considered by MacGillivray to include the Emphytinae, Selandriinae, and the Lycaotinae, by Rohwer (47) these three plus the Allantinae. MacGillivray (38) placed *Lycaota* in a separate subfamily close to the Blennocampinae on the basis of the medio-cubital cross-vein. Rohwer placed the genus in a separate tribe in his Emphytinae (equal to the Blennocampinae). Ross (52), regarded the Lycaotinae as a subfamily, "a small group which is undoubtedly the present day representative of the ancestor of the Tenthredininae". In this he followed his own detailed analysis of the group made in 1932 (49), in which he emphasized that "the pedicellate condition of the first anal cell in the Blennocampinae arose from the condition existing in the Selandriinae and Emphytinae, not from the condition exhibited by *Lycaota* which is typical of the condition found in a large number of the Tenthredininae". Benson (4) stressed that in two additional characteristics of the Tenthredininae, "the form of the cervical sclerites and the relationship between the basal and cubital veins in the fore-wing", the Lycaotinae not only disagree with the Tenthredininae but agree most closely with the Blennocampinae. These facts prompted him to include the "Lycaotinae" as a separate tribe in the Blennocampinae. In his latest revision, Ross (53) was in agreement. His placing of the Lycaotini as the first tribe in the Blennocampinae stresses the primitive nature of the group, and recalls the strong similarity of the Tenthredininae and the Blennocampinae and the problem of the origin of the former (Ross, 52).

Internal anatomical results confirm the primitive position of the *Lycaota* group, a position similar to that postulated for the Selandriinae, Dolerinae, and the Athaliinae. There is no internal basis for including it in the Blennocampinae, without assuming that *Lycaota* maintains an even more anomalous position in the Blennocampinae than do *Dimorphopteryx* and *Allantus calceatus* in the Allantinae.

It is interesting that Benson (8) includes the *Athalia* group as a tribe in his enlarged Blennocampinae, regarding it as a primitive group (originally a tribe in his Emphytinae equals the Allantinae). Among the general similarities to be found, the Athaliinae and the *Lycaota* group are almost identical in the possession of two longitudinal grooves, one on each side of a deep middle groove in the labrum which suggests a close relationship of the two close to the roots of the Blennocampinae and the Allantinae, and as will be seen, the Tenthredininae. On the basis of internal anatomy, the writer, however, favours reinstatement of subfamily status for *Lycaota* and the grouping of the Lycaotinae with the Selandriinae-Dolerinae-Athaliinae as four primitive subfamilies of the Tenthredinidae.

Tribe Blennocampini

Tomostethus multicinctus (Rohwer). (Det. H.H.R.). Host, *Fraxinus* sp. Location, Ottawa, Ont., Canada. Figs. 106, 146.

- A. 1. Pharynx, narrow; oesophagus slightly globular, enlarged into broad crop. Histologically slight difference in cells of lateral oesophageal flaps. No true oesophageal invagination.
2. Mid-gut stocky, extends uniformly to junction with hind-gut, lightly marked anteriorly by transverse striations. Histologically entire epithelium thrown into loose folds, pattern changes mid-way in gut. Gradual transition from tall cylindrical cells near fore-gut, to lower cylindrical-to-oval cell type for most of the gut, and finally to a more rectangular cell-type near the end of the mid-gut.
- B. Two separate stalks enter gut, each squat somewhat L-shaped, one axis anteriorly directed, the other laterally and dorsally. From each anteriorly directed arm, three tubules extend anteriorly. From base of each L-shaped stalk three or four tubules extend posteriorly floating freely in the rectal body cavity. The L-shaped stalk may be constricted laterad of the two inner tubules.
- C. Salivary glands single pair of main, two or three pairs of accessory. Single row gland cells down each side of main duct, join duct in twos.
- D. Extensive fat sheath over gut and salivaries, separate smaller sheath over salivaries alone.
- E. Epidermal glands noted, hollow spine-like processes. Surface glandulae present.
- F. Endocuticle thick, exocuticle moderately thick, epicuticle thin. Numerous conical spinous processes correlated, probably epidermal glands connected, noted as cuticular projections.

Tomostethus nigritus (Fab.). (Det. R.B.B.). Host, *Fraxinus* sp. Location, England. Fig. 107.

Strikingly similar to *T. multicinctus*, except:

- B. Line of main axes of two common stalks at 45° angles to mid-ventral line, sloping latero-posteriorly; approximately four anteriorly directed tubules from the anterior half, two lateral from the middle and five posteriorly from the posterior half; may be variation of a tubule or two but pattern constant in a semicircle arrangement, tubules almost constricted at base.
- C. Single pair of accessory glands present.

Pareophora minuta (MacGillivray). Host, *Fraxinus* sp. L. Location, Ottawa, Ont. Fig. 108.

As in previous two, except:

- B. Line of main axes of two common stalks at right angles to mid-ventral line. Two anterior branches from each stalk, then stalk extends laterally and latero-posteriorly to give rise to three tubules, of which two may turn posteriorly and are lightly bound to the rectum.
- C. Slight indication of alternate junctions and bulb-like expansions in duct; no reservoir; gland cells round. Single pair of accessory glands present.

Rhadinoceraea micans (Klug). (Det. R.B.B.). Host, *Iris* sp. Location, England. Fig. 109.

- B. Two main bulbous stalks fuse just before entrance to gut, main axes parallel to mid-ventral line, three branches lead anteriorly, as in all Blennocampinae so far examined (resembling three anterior-tubule arrangement, in Allantinae). These anterior branches may subdivide. Lateral extensions of main bulbous stalks send three tubules posteriorly.
- C. Indication of alternate bulb-like expansions in the salivary ducts; no reservoirs; round gland cells.

Phymatocera aterrima (Klug). (Det. R.B.B.). Host, *Polygonatum* sp. Location, England. Fig. 110.

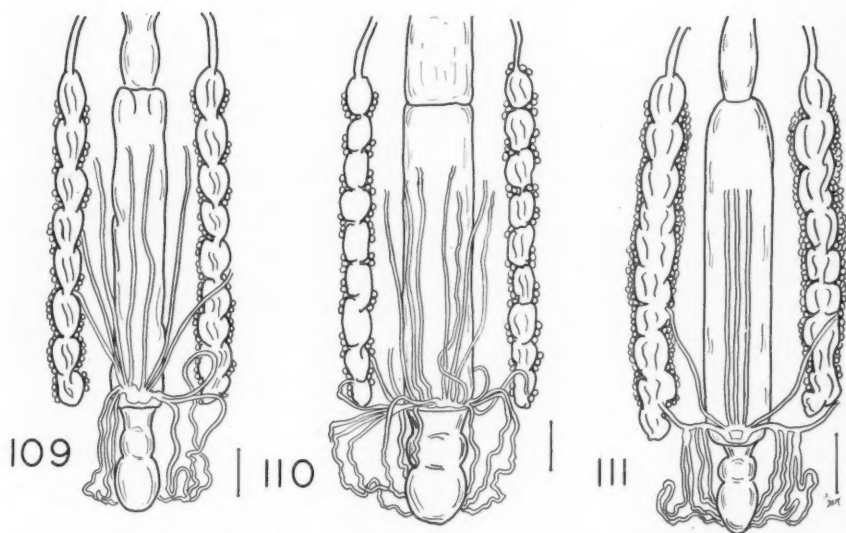
- A
 - 1. Crop very large.
 - 2. Mid-gut "fuzzy" surface.
- B. Malpighian arrangement very similar to that of *Tomostethus nigratus* except the base line of two common stalks fused and drawn out at 90° to mid-ventral line. On each side of mid-line, three anterior, two latero-anterior, and five or six posterior tubules, somewhat variable in number.
- C. Salivary glands, single set of main, definite alternation of round, bulb-like expansions and narrow junctions, round gland cells.
- D. Thick fat sheath encasing salivary glands and gut.
- E. Occasional glandubae on surface.
- F. Moderately thick cuticle, large, protruding spines with connected epidermal cells, glandular function suspected. Glandubae on posterior body surface.

Periclista sp. Host, *Quercus alba* L. Location, Ottawa, Ont., Canada. Fig. 112.

- A
 - 1. Pharynx narrow; oesophagus slender, crop fairly large, no trace histologically of oesophageal invagination.
 - 2. Mid-gut slender, unmodified tube, very little epithelial cell variation. Cells tall, rectangular.
 - 3. Hind-gut with limits of ileum, colon, and rectum indistinct. Histologically cells of colon flat, those of rectum square to rectangular.
- B. Malpighian arrangement essentially that of *Tomostethus multicinctus*. However, two inner tubules may be separated by constriction or may enter gut separately.
- C. Salivary glands, single pair of main, two small pairs of accessory. Main ducts with alternate bulb-like expansions and narrow junctions. Gland cells large, irregularly shaped, single row along each side of duct, attached individually or in twos.

Periclista albida (Klug). (Det. R.B.B.). Host, *Quercus* sp. Location, England. Fig. 111.

- A
 - 1. Crop moderate size.
 - 2. Mid-gut narrow.

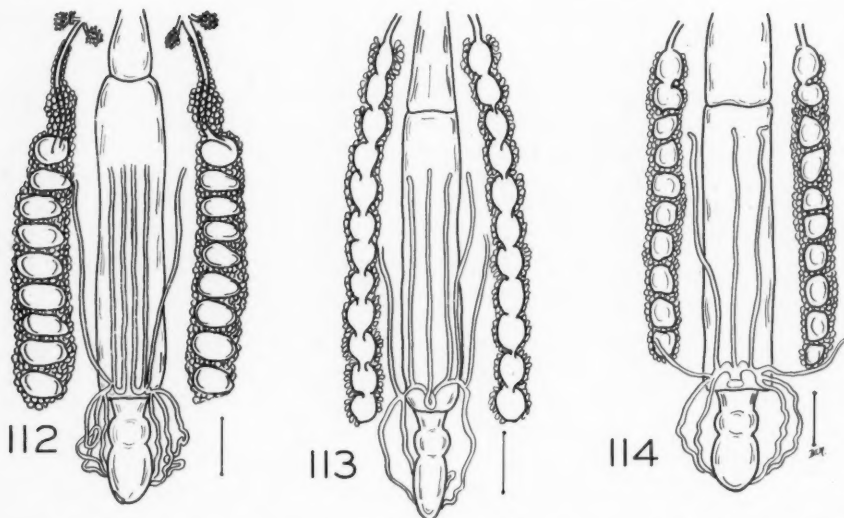


Figs. 109. *Rhadinoceraea micans* (Klug). 110. *Phymatocera aterrima* (Klug). 111. *Periclista albida* (MacGillivray).

- B. Malpighian arrangement reminiscent of that of *Ametastegia* (*Ametastegia*) *equiseti* and of *Tomostethus* spp. Peculiar fusion of 2 slender common stalks, single entrance to gut, region of fusion filled in lightly in centre (outlines of stalks apparent) and anterior edge of this fused body crossed by transverse connecting stalk. From transverse connecting stalk arise three anteriorly directed tubules, one on mid-venter, two close on either side; and one antero-lateral tubule bound in salivary gland. Lateral wing of stalk gives rise to one lateral tubule bound in end of salivary gland, and to four posteriorly directed, perirectally bound tubules, the two outermost joining in swollen base.
- C. Salivary glands single set main, alternate bulb-like expansions and junctions along ducts, squared gland cells in clusters of two to five along ducts.

Blennocampa pusilla (Klug). (Det. R.B.B.). Host, *Rosa*, sp. Location, England. Fig. 113.

- A. 1. Crop extremely large.
2. Mid-gut uniform.
- B. Malpighian tubule arrangement resembles that of *Periclista albida*. Again two common Malpighian tubule stalks fuse just before entrance to gut. Entrance fairly far anteriorly and indication of intermediate sac-like flap into which the stalk empties, line of fusion at level of transverse connecting stalk of *albida*. One large branch tubule extends anteriorly along the mid-ventral line, single branch tubule on either side. From lateral leaf-like extension of stalk arise three tubules divided between anterior and posterior extension.
- C. Salivary glands, single set of main, ducts show alternation of bulb-like expansions and narrow junctions, emphasis on large, almost telescoped, bulbs. Flattened salivary cells.



Figs. 112. *Periclista* sp. 113. *Blennocampa pusilla* (Klug). 114. *Monophadnoides geniculatus* (Hartig).

Monophadnoides geniculatus (Hartig). Host, *Rubus*. Location, Ottawa, Ont., Canada. Fig. 114.

A 1. Similar to *Blennocampa pusilla*.

B. Malpighian tubule arrangement resembles that of *Blennocampa* in particular. Two common stalks fuse just before entrance to gut. Third stalk overlaps and fuses with the former at the entrance, the three forming a globular body with the central portion thinned out, only stalks making up the framework standing out. Two lateral stalks extend laterally sending off two anteriorly extending branch tubules, continue latero-posteriorly, may or may not divide, pass posteriorly where loosely bound perirectally. Central stalk continues anteriorly along mid-ventral line.

C. Salivary glands, single pair of main, striking bulb-like expansions alternating with narrow junctions along the gut. Gland cells very large, square to pear-shaped, similar to those of *Athalia* spp. Thick coating of cells about duct enter in clusters of from two to four cells.

Yuasa (69) considered the "Blennocampini", as set off by MacGillivray, to be a large subfamily, rich in genera and species, and closely related to the Fenusinae and Scolioneurinae. This was in agreement with Konow's (36) arrangement, except that the latter placed the "Blennocampides", third in his "Tenthredinini". Rohwer (47), on the other hand, included all the genera, except *Tomostethus* and *Phymatocera*, in the Empriinae. His division was based on the two genera possessing a prepectus and, however valid or invalid, it proved useful in larval classification, since larvae of *Tomostethus* and *Phymatocera* differed from all other blennocampids then known in lacking characteristic spines. Ross (52) also states of the Blennocampinae "separation of genera is difficult due to a lack of outstanding characters upon which to base phylogeny". The salivary ducts of the blennocampids are variable: two species of *Tomostethus* have straight

ducts of uniform diameter, and round gland cells; the remaining species show definite indications of alternations into bulbs and narrow junctions. In overall appearance there is a marked similarity in the duct arrangement in the Caliroini and Blennocampinae, with bulb-like expansions along the length. The trend from uniform glands to bulb-like expansion in the blennocampids parallels in lesser degree that found in the Allantinae and the Selandriinae.

Within the Blennocampinae the most interesting trends are apparent in the Malpighian tubules as will be seen in the discussion. The general arrangement of the tubules of the Blennocampinae (variations of a *Tomostethus*-like arrangement of three anterior and four or five latero-posterior tubules on each side) is very similar to that of the Allantinae generally, or of the Empriini grouping particularly, thus providing unusually strong confirmation of Rohwer's insistence that the blennocampids should (except for *Tomostethus* and *Phymatocera*) be included in the "Empriinae". In this case however, *Tomostethus* and *Phymatocera* definitely form part of the series concerned. Once again two possibilities arise; either parallel evolution has occurred in two extremely closely related subfamilies, or the two are a single entity showing simple variation in the same theme, i.e. the Malpighian tubule arrangement. *Ametastegia equiseti* and *Periclista albida* are almost identical in general tubule pattern; the former, however, has the "3 by 1" arrangement typical of the Empriini, the latter a modification of the *Tomostethus*-formation. *Monostegia abdominalis* and *Rhadinoceraea micans* are close enough on internal anatomical grounds to be congeneric. *Allantus cinctus* in the Allantini, resembles *Periclista* sp. in the Blennocampinae. *Pseudosiobla* of the Eriocampini resembles, as has been shown, the Empriini type of Malpighian arrangement as well as that of certain of the Blennocampinae e.g. *Blennocampa pusilla* and *Rhadinoceraea micans*. Benson's (8) change from his 1938 classification involved a fusion of the Emphytinae (Allantinae) and Blennocampinae with the Caliroini and Fenusini of the old Heterarthrinae to form the new Blennocampinae. It now appears that not only does parallel evolution show up as a general tendency of the tubules, (e.g. towards perirectal binding or towards fusion and single entrance to the gut—with the result that certain species such as *Cimbex* and *Arge* might be said to be at roughly the same level of Malpighian tubule evolution as *Macremphytus* of the Allantinae) but that some of the suggested parallels in different subfamilies (e.g. the Heterarthrinae, Allantinae, and Blennocampinae) are actually variations within a single group. It is difficult to escape the fact that anatomical characteristics in the subfamilies in question are in the latter category, for the findings are in striking agreement with Benson's suggested grouping. The possibility that the Tenthredininae may also be involved is examined in the following section.

Subfamily Tenthredininae

Lagium sp. (Det. H.H.R.). Host, Unknown. Location, Palos Hills, Idaho, United States. Fig. 115.

- A 1. Pharynx, narrow; oesophagus enlarging into huge crop extending to third abdominal segment.
2. Mid-gut wide, stocky, transversely striate for entire length.
- B. Malpighian tubules, two anteriorly directed main stalks enter mid-gut, one on either side of mid-ventral line. Each stalk splits into group of eight anteriorly-directed tubules, four lateral tubules turning posteriorly, and one tubule directed posteriorly. The stalk is constricted at the base of the seventh tubule from the mid-ventral line and the first four anteriorly-extending tubules are superimposed two on two. The "sun-burst"

Malpighian arrangement of *Lagium* is typically tenthredininine, resembling most closely the general *Tenthredopsis* pattern.

- C. Salivary glands, single set of main, small pair of accessory. Ducts are uniformly broad although not expanded to full extent in specimen observed, and are bordered by two double rows of round, medium-sized salivary gland cells.
- E. Tall cone-shaped, protruding glands give general warty appearance to the cuticle.

Ross (52) states that in the development from the more primitive to the more specialized genera in the Tenthredininae, the eyes, mandibles, and cervical sclerites have evolved together. *Lagium* and *Aglaostigma* are among the more primitive groups as far as adult characters are concerned. Internal anatomical detail points to a general trend in the Tenthredininae from a crescentic, "sun-burst" Malpighian tubule arrangement characterizing the acceptedly primitive genus *Tenthredopsis* to a more compact grouping in *Tentredo* and *Macrophya*. *Lagium* conforms with a primitive Malpighian pattern.

Aglaostigma lichtwardti Konow. (Det. J. Pasteels). Host, *Petasites* sp. Location, Belgium. Fig. 116.

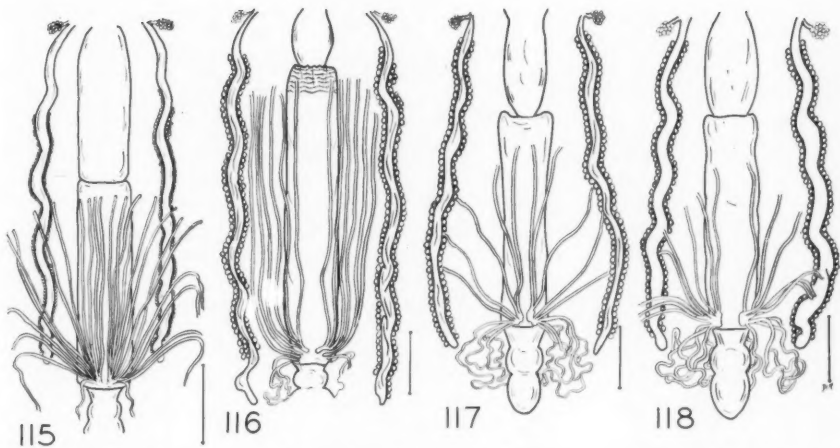
- A 1. Pharynx, slender; oesophagus expanded into large crop stretching to third thoracic segment.
- 2. Mid-gut uniform tube strongly striate anteriorly, traces of five deep transverse folds.
- B. Malpighian tubules exerted at three levels, approximately eight separate entrances. At the antero-ventral level, four tubules on each side branch from common stalk at 45°, proceed forward; at the middle level, two latero-anterior tubules either fuse or enter gut separately; at the postero-dorsal level, two directed posteriorly may fuse. Tubules at each level characterized by a "layered" effect as well, e.g. the superposition of two upon two others, recalls the layered effect of the tubules in *Cimbex*.
- C. Salivary glands, single set of main, small pair of accessory; main ducts wide, uniform. Gland cells large, rounded.

Aglaostigma is considered as being among "the more generalized" of the Tenthredininae by Ross (52) on the basis of adult characters (bidentate mandibles, small eyes, etc.). Of the seven species recognized in North America, much synonymy may be involved. Benson (8) groups *Tenthredopsis* and *Aglaostigma* in the Tenthredopsini as the sole genera.

Tenthredopsis litterata (Geoffroy). (Det. R.B.B.). Host, *Gramineae*. Location, Scotland. Fig. 117.

- A 1. Crop huge.
- 2. Mid-gut short, stocky, unmodified.
- B. Malpighian tubules similar to *Aglaostigma* in arrangement except that each of two main stalks more deeply constricted. Close resemblance to arrangement in *Tomostethus nigrinus*.
- C. Salivary glands as in *Aglaostigma*.

Among the five British species of *Tenthredopsis* there are apparently three distinct species groups (Benson, 8); in one the species *coquebertii*, *friesei*, and *nassata* are separable with difficulty on the basis of adult male genitalia, and almost identical as larvae. Specimens of *litterata*, very close to this group, and of *nassata* were alone available for internal study.



Figs. 115. *Lagium* sp. 116. *Aglaostigma lichtwardti* Konow. 117. *Tenthredopsis litterata* (Geoffroy). 118. *Tenthredopsis* sp. 1.

Tenthredopsis sp. 1. Host, Unknown. Location, Sault Ste. Marie, Ont., Canada. Fig. 118.

A 1. As in *litterata*, crop enormous.

B. Malpighian tubules, bases of two main stalks parallel, fairly widely spaced; tubule arrangement semi-circular. Tubules in three groups, five anteriorly, three latero-ventrally, four posteriorly. Some tubules superimposed over others,—a general tendency in *Tenthredininae*.

The species falls into the genus *Tenthredopsis* in Yuasa's key to the genera of the *Tenthredininae* and resembles *T. litterata* in general group characters.

Tenthredopsis nassata (L.). (Det. R.B.B.). Host, *Gramineae*. Location, Scotland. Fig. 119.

B. As in *Tenthredopsis* sp. 1, except two main stalks fused in smooth semi-circle across mid-ventral edge of junction of mid- and hind-gut. Five anterior and lateral, three or four posterior branches from semi-circle on each side.

Tenthredopsis sp. 2. Host, *Gramineae*. Location, Sault Ste. Marie, Ont., Canada. Fig. 120.

A 1. Crop, huge, extending to or beyond second abdominal segment.

B. Malpighian tubules exceedingly close to arrangement in *Tenthredopsis nassata* except six anteriorly extending on each side, two latero-anteriorly and three or four posteriorly.

Larva close to Yuasa's description of *T. semilutea* Norton.

Although the genus *Tenthredopsis* was recognized by Yuasa, his *semilutea* Norton, the only *Tenthredopsis* larvae available to him, has been included by Ross (52), with the old genus *Kincaidia* MacGillivray, in the genus *Aglaostigma*. Since the species examined by the writer were provided by Benson and since he separates the genera *Aglaostigma* and *Tenthredopsis* (8), his terminology is followed and the two North American larval forms, which resemble the British *Tenthredopsis*, are considered as members of that genus.

Tenthredo colon Klug. (Det. R.B.B.). Host, *Epilobium hirsutum* L. Location, England. Fig. 121.

A 1. Crop huge, extending to approximately second abdominal segment.

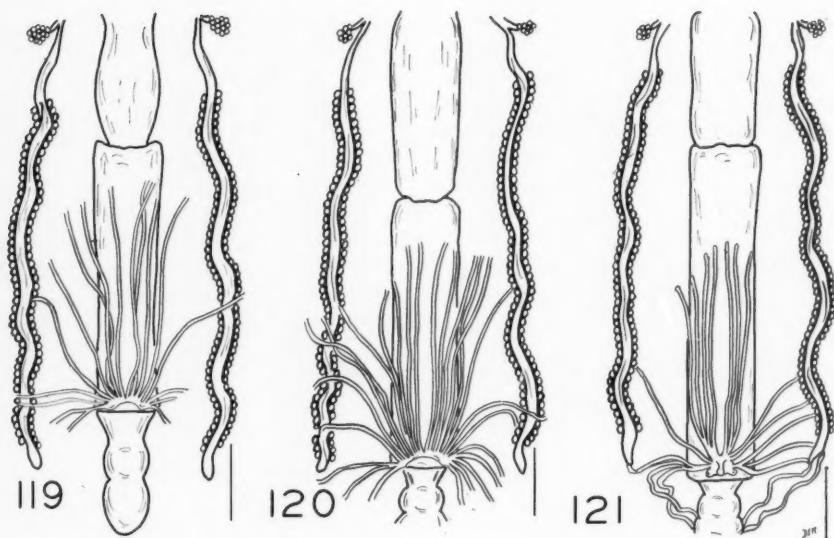


Fig. 119. *Tenthredopsis nassata* (Linnaeus). 120. *Tenthredopsis* sp. 2. 121. *Tenthredo colon* Klug.

- B. Malpighian tubules with two main stalks fusing, with sac-like medial region, single entrance to gut; eight tubules each side, three, occasionally, four anterior, one or two lateral, and three posterior. Occasionally as illustrated four anterior, one latero-anterior, three posterior.
- C. Salivary glands when emptied of secretion, irregular in outline. Gland cells join ducts in groups of four or five.

Ross (52) considers the genus *Tenthredo* to be a highly specialized member of the Tenthredininae (quadri-dentate mandibles, large eyes, etc.). He adds that *Tenthredo*, one of the largest of sawfly genera, has evolved along many specialized lines in several parts of the world thus forming a large number of distinct phylogenetic units that are separable sometimes, and then only imperfectly, on male genitalic characters. He implies it best to regard the units as subgenera pending examination of the world fauna. Benson (8), stresses that any segregation he himself makes within the genus is on the basis of artificial colour groups and thus only for convenience in keying. *Tenthredo* and *Rhogogaster* make up Benson's Tenthredinini.

Tenthredo obsoleta Klug. (Det. R.B.B.). Host, *Plantago lanceolata* L. Location, England and Scotland. Fig. 122.

- A 1. As in *T. colon*.
- 2. Mid-gut deeply anteriorly delimited by longitudinal folds.
- B. Two large, expanded main stalks fuse before common entrance. From each stalk, four anterior tubules, five antero-lateral, three or four posterior. Arrangement very similar to that of *Monostegia abdominalis* and *Rhadinoceraea micans* except for tubule number.

***Tenthredo scrophulariae* L.** (Det. R.B.B.). Host, *Scrophularia aquatica* L. Location, England. Fig. 123.

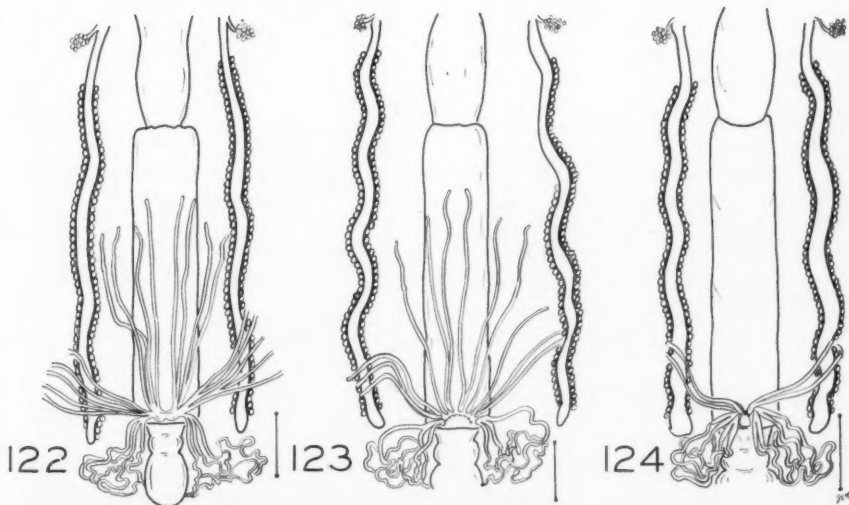
- B. Semicircular tubule arrangement across mid-ventral line. Tubule entrances mostly separate: three anterior tubules, three antero-lateral, and three or four posterior with fused entrance.

***Tenthredo zona* Klug.** (Det. R.B.B.). Host, *Hypericum perforatum* L. Location, England. Fig. 124.

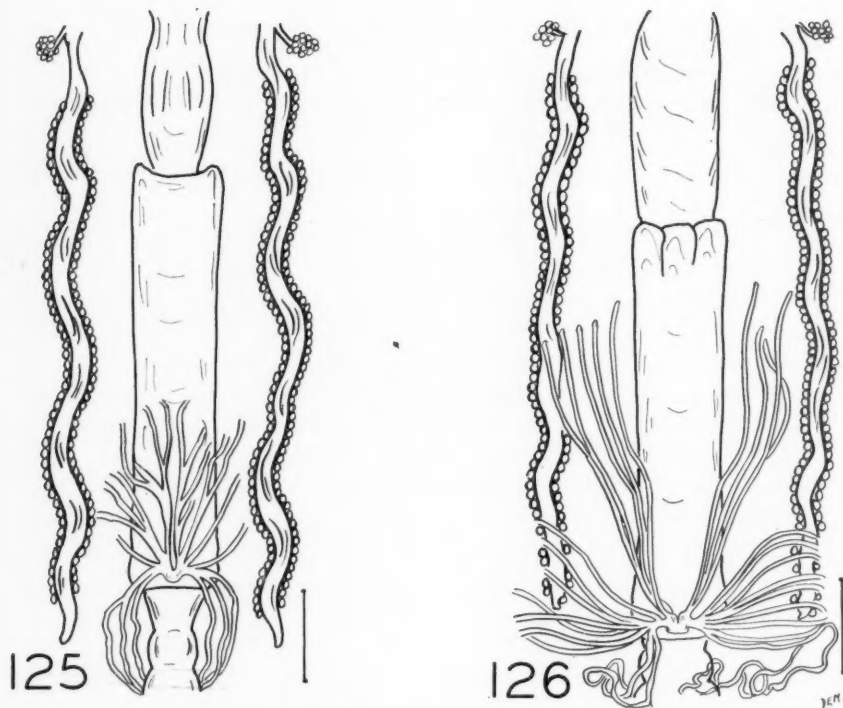
- B. Single, wide, common stalk, peculiar wedge-shape, extends anteriorly, slightly narrowed. At anterior constriction, branch stalk from each side gives rise to two antero-lateral tubules and basally to four posterior tubules, each swollen at origin. Arrangement generally similar to that of *Monophadoides* and *Macremphytus* spp. 2 and 3.

***Tenthredo* sp. 1.** Host, Unknown. Location, Ottawa, Ont., Canada. Fig. 125.

- A 1. Pharynx, narrow; oesophagus, large, pear-shaped, deeply longitudinally striate, expanded into fairly large crop. Pronounced oesophageal invagination in section.
2. Mid-gut uniform, lightly transversely-striate for entire length.
- B. Single, wide basal stalk divides into anterior, lateral, and posterior branches; anterior branch comprises four tubules entering at successive distances from basal stalk; lateral branch gives rise to three tubules, branching variable; posterior branch comprises one lateral and three posterior tubules. Branching may continue in the secondary tubules, similar to the ramifications found in the Cimbicidae.
- C. Salivary glands, single pair of main, small pair of accessory. Gland cells individually attached in rows along unmodified ducts.
- C. Salivary glands and gut separately encased in fat sheath.
- E. Surface glandubae present.



Figs. 122. *Tenthredo obsoleta* Klug. 123. *Tenthredo scrophulariae* Linnaeus.
124. *Tenthredo zona* Klug.



Figs. 125. *Tentbreda* sp. 126. *Macrophya epinota* Say.

There is striking similarity in antler-like branching in *Eriocampa ovata* and *Tentbreda* sp. 1. The uniformity of the internal anatomical features of the species of *Tentbredopsis* and *Tentbreda* indicates a similar degree of specialization of the two genera.

***Macrophya epinota* (Say).** Host, *Sambucus* sp. Location, Sault Ste. Marie, Ont., Canada. Fig. 126.

The larvae key to Yuasa's rather obscure description of the larva of *M. epinota*. "*Macrophya epinota* (Say)", denotes a complex of unworked, but generally similar, forms in Ross (50, 51).

- A. 1. Crop, huge, extending to second abdominal segment.
2. Mid-gut, deeply delimited anteriorly by longitudinal folds, remainder unmodified.
- B. Single wide partly cleft basal stalk with anterior and lateral branches; each anterior branch with four or five anteriorly directed tubules and each lateral branch with nine tubules, two of which are directed posteriorly, the balance laterally. The superposition of tubules is most pronounced.
- C. Slightly irregular duct outline.

Yuasa states that the Tenthredininae are the second subfamily in the series of specialized Tenthredinidae (Phyllotominae being his first), and adds that in many cases the larvae resemble those of the Emphytinae (Allantinae). In discuss-

ing the "generalized" subfamilies, he stressed that the Emphytinae, with six annulets, were nevertheless very close to the Selandriinae and Tenthredininae, each with seven annulets.

Benson (4) says of the Tenthredininae "Except for a few isolated often monotypic genera, the great abundance of closely related species are difficult to divide into satisfactory genera at all". He (8) excludes the Tenthredininae from his enlarged Blennocampinae (equals Blennocampinae-Allantinae-Caliroini-Fenusini of the Heterarthrinae-Heterarthrini) because he considers that their similarities are purely superficial, representing the results of parallel evolution in quite separate groups.

The salivary glands of all species of Tenthredininae are of similar type to those of the advanced Nematinae and of the Blennocampinae-Allantinae-Heterarthrinae. Therefore they are of no value in determining the affinities of the Tenthredininae and the enlarged Blennocampinae.

Similarity in the tubule arrangements of species of the Tenthredininae and various members of the "Allantinae" and "Blennocampinae" has been drawn throughout the preceding section, individual deviations being merely variations of a broad pattern common to the three subfamilies. To separate the components as "superficially similar" subfamilies distorts the meaning of their association within the family Tenthredinidae and obscures their relationships with other families. That the species in the subfamilies in question have been frequently confused and their systematic position shifted from one grouping to another indiscriminately are indications that great homogeneity exists and that evolution in the various groupings is either incipient (as in the Diprionidae) or that the variability evolved is infinitesimal. The question as to further arrangement in the Tenthredinidae will be viewed in the conclusions.

On the basis of internal larval anatomy, the following three-way division of the Tenthredinidae is suggested:

- (1) Selandriinae-Dolerinae-Athaliinae-Lycaotinae;
- (2) Nematinae;
- (3) Blennocampinae-Allantinae-Heterarthrinae-Tenthredininae.

SUPERFAMILY SIRICOIDEA

Family Siricidae

Subfamily Siricinae

Sirex noctilio (Fab.). (Det. R.B.B.). Host, *Pinus* sp. Location, England. Fig. 127.

- A 1. Pharynx, slender; oesophagus, bulbous, enlarging into fairly muscular crop.
2. Mid-gut, slender, unmodified, widening gradually posteriorly.
3. Hind-gut divisions, indistinct, rectum large.
- B. Eight tubules entering separately, four ventral curve posteriorly short distance, then anteriorly and float freely in body cavity. Four dorsal extend posteriorly, loosely attached to rectum. Short stub of odd tubule projects from mid-dorsal line.
- C. Salivary glands difficult to locate. Single pair of slender squared ducts widening posteriorly into rectangular glandular body.

Sirex cyaneus (Fab.). (Det. R.B.B.). Host, *Pinus* sp. Location, England. Fig. 128.

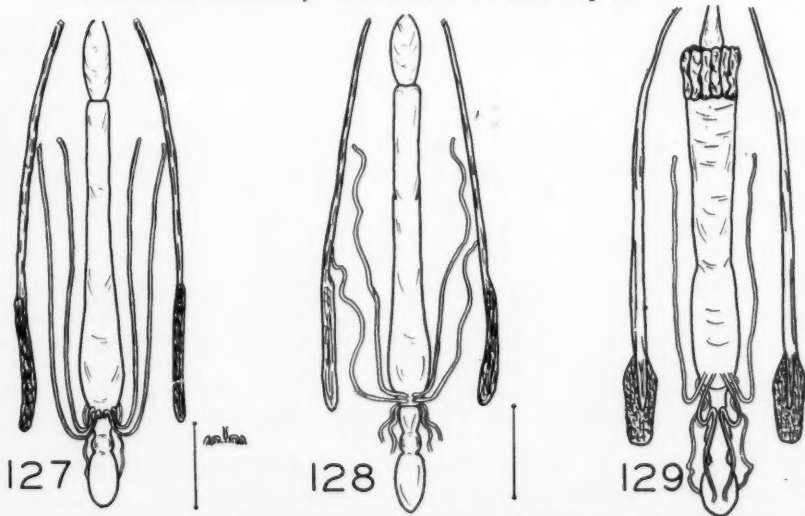
- A 1. As in *S. noctilio*.
- B. Eight tubules entering separately, four ventral, two on each side mid-ventral line, one anterior to other, directed laterally, then anteriorly,

floating freely in the body cavity; four dorsal, two on each side of mid-dorsal line, one anterior to the other. The anterior pair circle the gut and extend posteriorly, loosely bound perirectally; the posterior pair extend directly posteriorly.

Subfamily Tremicinae

***Tremex columba* (L.).** (Det. H.H.R.). Host, *Acer* sp. Location, Illinois, United States. Fig. 129.

- A 1. Pharynx, narrow; oesophagus, slender, expanded into wide crop near junction with mid-gut.
2. Mid-gut, slender, unmodified, first one-sixth characterized by approximately 12 deep longitudinal folds, raised in series of pouches, appearance of gastric diverticula with glandular function.
3. Hind-gut enlarged to rectum; limits of ileum indistinct; globular colon; large rectum.
- B. Six tubules, four ventral and two latero-ventral. Two outer ventral tubules extend posteriorly to level of colon, turn anteriorly, floating freely. The remainder extend posteriorly, coiling loosely, bound lightly to hind-gut in position illustrated.
- C. Salivary glands single pair of main, two small pairs of accessory (latter extremely small, not illustrated). Main ducts square to rectangular, extend almost to end of mid-gut; in this region, ducts surrounded by gland cells forming two large, compact, club-shaped bodies encased in common sheath. Modified squared collecting duct extends almost to gland limits as definite core, in contrast with the fairly irregular duct outline in the pamphiliids.
- D. Entire abdominal tract, salivary glands, and Malpighian tubules covered by extremely thick fat body.
- F. Cuticle scaly appearance, marked ovoid outlines from underlying epidermal cells marked by small clusters of minute spicules.



Figs. 127. *Sirex noctilio* (Fabricius). 128. *Sirex cyaneus* (Fabricius). 129. *Tremex columba* (Linnaeus).

One of the relatively few points of agreement between systematists is found in the Siricoidea. There are minor differences such as Ross' (52) elevation of the Cephidae to superfamily level and Benson's (8) consideration of the Orussidae as a superfamily. Ross (52) divides the superfamily into four well-marked families, Syntectidae (Syntexidae of Benson, 4), Xiphydriidae, Siricidae, and Orussidae.

Systematists agree also (a) that the Siricidae definitely merit family rank, (b) that the group contains genera and species well-defined from the day of Linnaeus, and (c) with Bradley's (12) subdivision of the family into two well-defined subfamilies, the Siricinae for woodborers in conifers and the Tremicinae for those in deciduous trees. Bradley stressed that the specific characters of some of the known species, e.g. *Tremex columba*, are subject to a wide range in variation, with several varieties described in detail for each. The antiquity of the Siricidae has been a long-debated topic (see Taylor, 63). Handlirsch (30) considered that the Siricidae evolved from an "osculant Jurassic group", and Morice (42) stated his "Primitive Siricid Line" theory thus: "We may suppose that the Siricidae are the earlier group but whether the Tenthredinidae and Lydini (Pamphiliidae) had Siricid ancestors, or whether the Siricidae plus Cephini plus Oryssidae and Tenthredinidae plus Lydini are respectively earlier and later branches of a common stock are questions which must be left unanswered." It might be added that the Siricid larvae appear to be more closely related to larvae of the controversial Orussidae than to those of the Cephidae or Xiphydriidae, according to Yuasa, who postulates a simple trend from the wood-boring to the parasitic habit. Yuasa adds that it would not be unreasonable to envision an independent evolution for the Orussidae, the family having arisen from the sawfly progenitor stock before the Xyelidae and Pamphiliidae originated.

The presence of anterior "gastric diverticula" in *Tremex* and the entirely smooth type of gut in the two *Sirex* spp., in addition to slight variations in tubule number and arrangement, suggest fairly well-defined anatomical differences, but whether of subfamily significance can not be determined until more members of each group have been examined.

The Siricinae are usually considered the more generalized, the Tremicinae the more specialized of the two subfamilies. The Malpighian tubules of the Siricinae recall the arrangement found in the Xyelidae and in other "primitive" species in different groups and the reduced numbers in the *Cephus* examined. *Tremex*, with much the same tubule arrangement, has a decreased tubule number indicative of a higher degree of specialization.

Family Xiphydriidae

Xiphydria prolongata (Geoff.). (Det. R.B.B.). Host, *Salix* sp. Location, England. Fig. 130.

- A. 1. Pharynx, slender; oesophagus, narrow, extremely long, muscular; no indication of crop expansion.
2. Mid-gut, wide, thickly transversely muscular.
- B. Eight tubules: six ventral enter in three pairs, v-shaped formation, extending anteriorly floating freely. Two dorsal tubules circle gut laterally to ventral surface then curl posteriorly, loosely bound perirectally.
- C. Salivary glands, single pair of main, each with anterior reservoir. Thick ovoid with pebbly surface; long slender sac includes the duct proper, and a thin lining of glandular cells. Strikingly similar to Pamphiliidae. Reservoir reminiscent of condition of Xyelidae.

Xiphydria camelus (L.). (Det. R.B.B.). Host, *Alnus* sp. Location, England. Fig. 131.

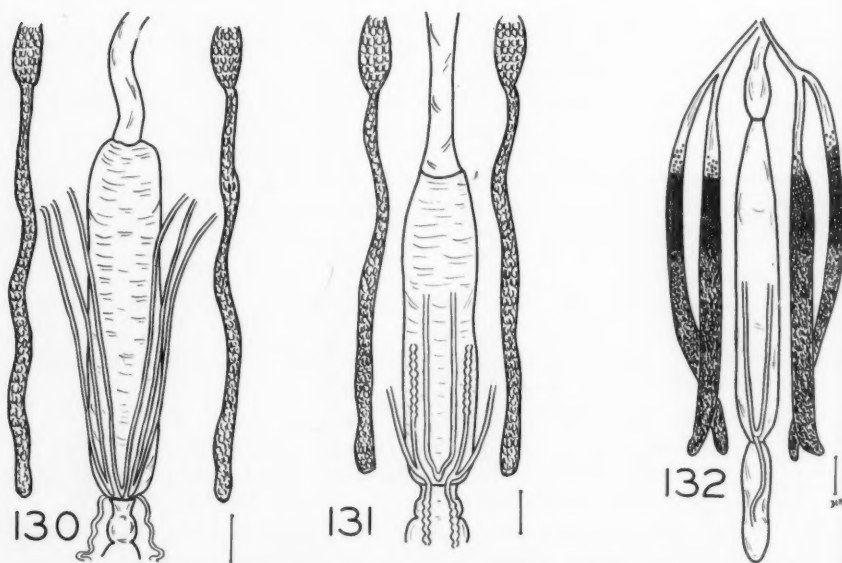
A 1, 2, 3. Proportion of fore- to mid-gut differs slightly from *prolongata*: in *camelus*, 1:2, in *prolongata*, 1:3.

B. Eight tubules enter ventral surface by three entrances. As in *prolongata*, the two middle tubules, V-shaped formation, extending anteriorly. Two anterior and one posterior fuse on either side forming Y-shaped structure. A suggestion of division of labour is seen in the convoluted structure of the distal half of the intermediate anterior tubules and also in the two posterior tubules.

The clumping of Malpighian tubules and the suggestion of a division of labour, point to *camelus* as the more advanced of the two species.

The Xiphydriidae are most closely related to the Syntectidae and to the Siricidae (once considered a subfamily of the latter). On venational characters, MacGillivray (38) assumed the Xiphydriidae to be the most generalized of specialized Tenthredinoidea. Ross (52) claimed that the Syntectidae with identical venation were even more primitive than the Xiphydriidae. In his subsequent revision (53) he considers the Siricidae to be intermediate between the Syntectidae and the Xiphydriidae.

The salivary glands of the Xiphydriidae show the incorporation of gland cells into the duct lining as in the other orthandrious families, Pamphiliidae, Siricidae, and as will be seen, the Cephidae, but not in the Xyelidae. The long sac-like secretory body in the Xiphydriidae is closer to that of the Cephidae and the Pamphiliidae than to the Siricidae. A reservoir is characteristic of the Xiphydriidae and Xyelidae, but not of the Pamphiliidae, Siricidae, and Cephidae, and might be indicative of a link between the two former families.



Figs. 130. *Xiphydria prolongata* (Geoffroy). 131. *Xiphydria camelus* (Linnaeus). 132. *Cephus cinctus* Norton.

SUPERFAMILY CEPHOIDEA

Family Cephidae

Subfamily Cephinae

Tribe Cephini

Cephus cinctus Norton Host, *Triticum*. Location, Manitoba, Canada. Fig. 132.

- A 1. Pharynx, narrow; oesophagus, pear-shaped, enlarged into crop.
- 2. Mid-gut, slender tube.* Low uniform epithelium.
- 3. Hind-gut, enlarged, cylindrical, undifferentiated.
- B. Three tubules enter mid-ventral line in Y-shaped formation, two anterior, one posterior.
- C. Salivary glands, two pairs of main extending at different levels in the body cavity, single pair of very small accessory (not illustrated). Each duct, surrounded by a thin, almost transparent sheath, increases slightly in diameter beyond second thoracic segment, continues posteriorly as fairly large sac, the true glandular region of the duct. Arrangement much as in *Pamphilius*, *Xyela*, and *Xiphydria*.
- D. Common abdominal sheath of fat-body and secondary sheath around gonads; separate sheath around posterior part of hind-gut.
- F. Cuticle fairly thick.

Benson (4) has divided the Cephidae into two subfamilies in his 1938 world survey which covered approximately 100 species in 11 genera. The writer examined *Cephus cinctus* and *Cephus pygmaeus* (L.) as well as material of *Janus luteipes* (Lep.). *C. pygmaeus* is identical with *C. cinctus* internally, but the internal anatomy of *Janus luteipes* proved indecipherable (specimens prepupal). To attempt to generalize on the basis of the anatomy of two species in a superfamily is dangerous, but *Cephus* must be described as typifying its group until more material is examined.

Ross (52) stresses that the Cephids are essentially sawflies but that "many specializations of the lower Apocrita beyond the sawflies have at least some expression in the Cephidae". The Cephidae, he believes, seem to stand in the line of advance to the primitive Apocrita. The Braconidae, the most primitive of the Apocrita, appear to have a cephid-like ancestor (52). The wing venation of the Cephidae is at the same primitive level as that of the Syntectidae and Xiphydriidae.

Yuasa is of the opinion that the Cephidae, on the basis of larval characters, are related to the Pamphiliidae and quite unrelated to the Xyelidae. Rohwer (47), on the contrary, felt that future studies would make it necessary to unite the Cephidae with the Xyelidae, treating both as subfamilies. No such union has subsequently been proposed. On the basis of wing venation, the Cephidae are, to MacGillivray (38), the most distinct of any group in his Tenthredinoidea and only indirectly related to any of the other families, being generalized in some, specialized in other features.

The salivary glands of *Cephus* are structurally very similar to those of the Pamphiliidae, and, except for lack of reservoirs, to those of the Xiphydriidae.

Table 5 is appended for comparison of anatomical details in the Megalodontoidae, Siricoidea, and Cephoidea, as well as the Blasticotomidae of the Tenthredinoidea.

*In morphological studies of the larvae of *Cephus cinctus*, Holmes (Can. Ent. 86: 159. 1954, and in personal correspondence) records the presence of a pair of gastric caeca at the junction of the fore- and mid-gut and of ten Malpighian tubules fusing before a common entrance to the mid-gut. The gastric caeca become non-functional and the ten tubules disappear following the final instar, preceding the true prepupal stage the following spring. The writer's descriptions of the two species of *Cephus* and of *Janus luteipes* are based on dissection of last-instar and early prepupal larvae.

TABLE V
Anatomical Characters of the Orthandria of Ross and the Blasticotomidae

	Salivary glands	Malpighian tubules	No. segments in antennae	Subanal appendages†
Megalodontoidea Xyelidae*	Reservoir, gland cells not incorporated in duct wall.	5-20 tubules, separate entrances, anterior and posterior	6	—
Pamphiliidae	No reservoir, gland cells incorporated posteriorly, not anteriorly.	Many tubules, partially fused before entrances, posterior only.	7	+
Siricoidea Xiphydriidae	Reservoir, gland cells incorporated.	8 tubules with V- or Y-shaped fusions, anterior and posterior.	3	—
Siricidae	No reservoir, gland cells incorporated.	8 tubules, separate entrances, anterior and posterior.	1	—
Cephoidea Cephidae	2 pairs salivaries, no reservoir, gland cells incorporated.	3 tubules, Y-shaped fusion, anterior and posterior, in last-instar and early pre-pupal larvae; 10 tubules in feeding stages.	4-5	+
Tenthredinoidea Blasticotomidae	Reservoir, gland cells incorporated	4 tubules, separate entrance, anterior and posterior	5	+

*10 pairs larvopods present, but lacking in all other groups; suranal process lacking in Xyelidae, but present in other groups.

†+ = present.

†- = absent.

DISCUSSION

In the present work, the groups represented by larval forms available for study were arranged according to the classification by Ross (53), and anatomical variations were searched for characters indicative of phylogeny. Factors considered in assessing the phylogenetic significance of anatomical characters include their usefulness in establishing separation within and between groups; their degree of progressive development within a group; persistence in form of the character despite variable body form adapted to specialized hosts or feeding habits. Characters selected as answering the requirements are primarily the salivary glands and the Malpighian tubules, and, secondarily or occasionally, such structures as the oesophageal and pharyngeal diverticula, gastric caeca, glandular crypt cells, eversible and non-eversible glands, and the fat body.

It was difficult to determine just what constitutes the primitive or the specialized stage of any phylogenetic character. One would expect that descriptions in postulated neuropteroid types and in the higher Apocrita could be accepted as delimiting the extremes of a particular character. Since there is little published information upon the comparative internal larval anatomy of any insect groups, and since the present work has not extended beyond the sawflies, these

extremes are not readily determinable. Judgment in defining the degree of specialization of a character has been modified in some cases by the appearance of the character in sawflies universally accepted to be primitive or highly specialized; and in others by the appearance of the character in other more primitive or highly specialized insects based on descriptions in the literature. Ross (52), Benson (4, 6, 7), and Yuasa (69), state that there is much parallel evolution within the sawflies and that while some characters in a species may be highly advanced, others may remain primitive. With these potential dangers in mind, deductions are made only when sufficient species have been examined to reveal an obvious trend, or where internal anatomy provides strong agreement or disagreement with the results of other workers.

Salivary Glands:

The few references available on the structure of salivary glands in larvae of the higher Hymenoptera suggest an incorporation of the gland cells into the lining of the duct, the whole being encased in a common sheath to form a fairly compact glandular body. The various characteristics of the glands in the different sawflies are summarized in Table 6 and shown diagrammatically in Fig. 151, which illustrates a concept of sawfly phylogeny with the salivary glands as the key character. A striking difference in salivary gland structure exists between the Orthandria and the Strophandria (*sensu* Ross, 52), momentarily omitting the Xyelidae and Blasticotomidae from consideration. In the Strophandria (Tenthredinoidea) Fig. 151, 3-13), there is an increase in cell number or a more elaborate cell arrangement with persistence of a narrow duct or there is a broad, expansible duct with small cells along its length. In the Orthandria (Fig. 151, 4-19), there is complete incorporation of the cells into the wall of the duct, the whole being encased in a common sheath to form glandular bodies of varying length.

The Xyelidae and Blasticotomidae (Fig. 151, 1 and 2) provide interesting examples of an arrangement intermediate between the free and incorporated gland cell condition, or more likely a primitive one from which the two main lines might have been derived. In view of the many character differences, it is reasonable to assume that the Blasticotomidae split off early from the main xyelid stem. Postulated derivatives from the Xyelidae-Blasticotomidae show a tendency towards broad expansible ducts (either alternate bulbs and junctions or uniformly wide ducts) in the first grouping (Tenthredinidae, Cimbicidae, Diprionidae, and probably Perginae); or towards non-expansible ducts with grape-like cell clusters or large, free cells individually joined in the second grouping (Argidae, Pterygophorinae, and Acordulecerinae). The Tenthredinidae subfamilies show all stages in a trend from an alternation of bulb-like expansions and narrow junctions, to a uniformly broad duct, while the Diprionidae and Cimbicidae have the broad ducts only. The "Pergidae", considered a family by Ross in his early key (52) and included in his second grouping with the Argidae (Fig. 149), belong, according to salivary gland structure, in the Tenthredinidae-Diprionidae-Cimbicidae complex or intermediate between it and the second group.

Simple modifications of an ancestral xyelid-type salivary gland towards the incorporation of gland cells, lead to the Pamphiliidae with their variability in number of salivary cells enclosed in a common sheath. The salivary glands hint at a more generalized or primitive position of the Xiphydriidae of the Pamphiliidae and at possibly a closer link with the Xyelidae. The sac-like formation in the Xiphydriidae resembles the duct and cell pattern of the Cephidae, while the latter, in turn, are not unlike *Pamphilius* in arrangement. In the Siricidae, the height of specialization in sawfly salivary glands is reached. As relatively

TABLE VI.
Salivary Glands.

Species	Res.	S. Duct	S. C. Att.	S.C.	S. G. Type
Xyelidae:					
<i>Xyela</i> , <i>Pleroneura</i> , <i>Macroxyela</i>	+	A.1	I	1	1
Pamphiliidae:					
<i>Acantholyda</i> sp. 1,2.....	-	LE.2	I	2	15
<i>Neurotoma</i>	-	LE.4	I	2	16
<i>Pamphilius</i>	-	E.2	I	2	14-15
<i>Cephalcia</i>	-	E.1	I	2	14
Pergidae:					
Acordulecerinae:					
<i>Acordulecera</i> , <i>Acorduleceros</i>	+	A.1	I	2	4
Perginae:					
<i>Perga</i> , <i>Cerealces</i>	-	B	I	5b	6
Pterygophorinae:					
<i>Lophyrotoma</i>	+	A.1	I	2	5
Argidae:					
Arginae:					
<i>Arge pectoralis</i> , <i>A. clavicornis</i> , 3 <i>Arge</i> spp.....		A.1	I & G	2	3A & B
<i>Arge annulipes</i> , <i>A. sugilloides</i> , <i>A. micheli</i> , <i>Arge</i> sp.1	+	A.1	G	2	3A
<i>Arge ochropus</i>	+	A.1	I	2	3B
Atomacerinae:					
<i>Atomacera</i>	-	A.1	I	2	3B
Sterictiphorinae:					
<i>Sterictiphora</i>	-	A.1	G.1	2	3 "A"
Sericocerinae:					
<i>Sphacophilus cellularis</i> , <i>S. plumiger</i>	+	A.1	G.1	2	3 "A"
<i>Sofus</i>	-	A.1	I & G.1	2	3 "A" & B
<i>Schizocera krugii</i>	+	A.1	G	2	3A
Blasticotomidae:					
<i>Blasticotoma</i>	+	A.1	I	2	2
Cimbicidae:					
<i>Zaraea</i> , <i>Abia</i>		B	I & C	5a	13
<i>Trichosoma</i> , 2 <i>Cimbex</i> spp.....	-	B	C	5a	13
Diprionidae:					
Monocteninae:					
<i>Monoctenus juniperinus</i>	-	B	I & C	5a	13
Diprioninae:					
10 <i>Neodiprion</i> spp., <i>Diprion</i> , 2 <i>Gilpinia</i> spp.....	-	B	I	5a	13
Tenthredinidae:					
Selandriinae:					
Strongylogasterini:					
3 <i>Hemilaxonus</i> spp.....	+	C.1	I	3	7
2 <i>Strongylogaster</i> spp.....	+	C.2	C	3	8
<i>Selandria serva</i>	-	C.2	I	3	10
<i>Aneugmenus</i>	-	C.2C.3	I	3	10
Dolerinae:					
4 <i>Dolerus</i> spp.....	-	C.1	I	3	7
Heterarthrinae:					
Caliroini:					
<i>Endelomyia</i> , <i>Caliroa fasciata</i>	+	C.4	I	3	11
<i>Caliroa cerasi</i>	+	C.4	C	3	11
Heterarthrini:					
<i>Heterarthrus</i>	-	B	I	5a	13
Fenusini:					
3 <i>Fenusia</i> spp., <i>Profenusia</i> , 2 <i>Metallus</i> spp.....	-	B	I	5a	13
<i>Parna tenella</i>	-	B	C	5a	13
Susaninae:					
<i>Susana</i>	-	B	I	5a	13
Nematinae:					
Cladiini:					
3 <i>Priophorus</i> spp.....	-	C.5	I	3	12
2 <i>Cladius</i> spp.....	-	A & B	I	3 & 2	3-5 & 13
<i>Trichiocampus</i>	-	A & C.5	I	2 & 3	3-5 & 12
Nematini:					
<i>Caulocampus</i> , <i>Hemichroa</i> , <i>Platycampus</i> , <i>Anoplonyx</i>	-	C.5	C	5a	12
4 <i>Pristiphora</i> spp., 2 <i>Pikonema</i> spp., 3 <i>Croesus</i>					
spp., 37 <i>Nematus</i> (<i>Pteronidea</i>) spp., <i>N. (Pon-</i>					
<i>tania</i>), <i>Amauronematus</i>	-	B	C	5a	13
<i>N. (Holcocneme)</i> , <i>Hoplocampa</i>	-	B	I	5a	13
Pseudodineurini:					
<i>Kerita</i>	-	B	I	5a	13

TABLE VI.
Salivary Glands—Continued

Species	Res.	S. Duct.	S. C. Att.	S. C.	S. G. Type
"Athaliinae":					
5 <i>Athalia</i> spp.	+	C.1	C	4	9
Allantinae:					
Allantini:					
<i>Empria</i> (<i>Parataxonus</i>)	—	B	C	3	13
<i>Monostegia</i> , <i>Amelastegia</i> (<i>Amelastegia</i>) 3 <i>Amelastegia</i> (<i>Protemphytus</i>) spp., <i>Amelastegia</i> on <i>Spiraea</i> , <i>Allantus cinctus</i> , <i>Macremphytus</i> sp. 1.	—	B	I	5a	13
<i>Allantus calceatus</i> , <i>Apethymus</i>	—	B	C	5a	13
<i>Macremphytus</i> sp. 2, 3.	—	C.3	I	6	10
<i>Macremphytus</i> sp. 4.	(—)	C.3	C	5a	10
Eriocampini:					
<i>Eriocampa</i>	—	B	C	5a	13
<i>Dimorphopteryx</i>	—	B	I	5a	13
<i>Pseudosiobla</i>	—	C.1	I	5a	10
Blennocampinae:					
Lycatini:					
<i>Lycota</i>	(—)	C.1	C	5a	10
Blennocampini:					
2 <i>Tomostethus</i> spp.	—	B	C	5a	13
<i>Pareophora</i>	—	C.5	I	5a	12
<i>Phymatocera</i>	—	C.1	I	5a	7
<i>Perichista</i> sp.	—	C.5	I	3	12
<i>Perichista albida</i>	—	C.1	C	6	7
<i>Blennocampa pusilla</i>	—	C.4	I	6	11
<i>Monophadnoides</i>	—	C.1	C	4	7
<i>Rhadinoceraea</i>	—	C.5	I	5a	12
Tenthredininae:					
<i>Lagium</i> , <i>Aglaostigma</i> , 4 <i>Tenthredopsis</i> spp.	—	B	C	5a	13
4 <i>Tenthredo</i> spp.	—	B	C	5a	13
<i>Tenthredo</i> sp. 1, <i>Macrophya</i>	—	C.5	I	5a	12
Siricidae:					
Siricinae:					
2 <i>Sirex</i> spp.	—	A.2	I	2	19
Tremicinae:					
<i>Tremex</i>	—	A.2	I	2	19
Xiphydriidae:					
2 <i>Xiphydria</i> spp.	+	D	I	2	17
Cephidae:					
2 <i>Cephus</i> spp., <i>Janus</i>	—	D	I	2	18

Res. — Reservoirs

— absent

+ present

(—) trace

S. Duct — Salivary Duct

A narrow in diameter

.1 round

.2 rectangular

B broad, expansible

C alternating bulb-like expansions and narrow junctions

.1 normal

.2 elongate junctions

.3 squared bulbs

.4 telescoped bulbs

.5 trace alternation effect

D complete incorporation of cells in duct wall.

E incomplete incorporation of cells in duct wall.

S.C. Att. — Salivary Cell Attachment

I individual

G grape-like branching

.1 short stalk grape branching

C clumped

S.C. — Salivary Cell

1. large rectangular

2. large round

3. flattened cuboidal

4. elongate-pear-shaped

5. (a) small, round, short stalk

(b) small, round, elongate stalk

6. small square

L looped duct

S.G. Type — Salivary Gland Type

Numbers taken from Fig. 151

few species have been examined in these families no attempt has been made to picture lines of descent (See Fig. 151) beyond general indications of possible evolution, e.g. Xyelidae to the Pamphiliidae, to the Cephidae; or Xyelidae to the Xiphidriidae, to the Pamphiliidae, on the one hand, and to the Cephidae on the other.

As seen in Table 6, reservoirs are found in the primitive species of nearly all groups. The reservoir characteristic is considered a primitive one that has been lost in the various groups with advance in salivary type. The ducts themselves are either round or rectangular in cross-section, a fundamental point for the separation of groups, including the Xyelidae and Blasticotomidae, with unincorporated gland cells from those with incorporated gland cells. Cell attachment, in clumps or individually, varies between species within a genus and accordingly the characteristic is of little importance for separation on a level higher than within the genus. Cell types follow the general descriptions as outlined (Table 6); the flattened cuboidal and elongate pear-shaped cells usually accompanying the alternate expansions and junctions duct type, or rarely the less specialized forms with the uniformly broad duct in this grouping.

Ross's fundamental division of sawflies into the Orthandria and Strophandria is on the basis of the male genitalia, the Xyelinae however being misplaced. Yuasa's division of sawflies is based on larvapods and sub-anal appendages but the Xyelinae, Blasticotomidae, Pergidae, and Argidae are anomalous groups based on these characters. The salivary glands serve as a broad general character of importance on a higher evolutionary level and provide clues to the proper position of these anomalous groups.

To summarize, the general trends are as follows: (the numbers are comparable to those used in Fig. 151.)

Salivary Glands: A. Square narrow duct, incorporated gland cells:

Pamphiliidae (14, 15, 16), Cephidae (18), Siricidae (19), Xiphidriidae (17).

B. Round narrow duct; many or large free gland cells:

1. Sheathlike—Xyelidae (1), Blasticotomidae (2), *Arge ochropus*, *Arge pectoralis*, *Sofus*, *Atomacera* sp. (3B).
2. Branching—Arginae (3A & 3B), Sericocerinae (3A), Sterictiphorinae (3B), Acordulecerinae (4), Pterygophorinae (5).

C. Expansible ducts, fairly small gland cells:

1. Alternating bulb-like expansions and narrow junctions, trend to straight ducts: Selandriinae-Dolerinae-Athaliinae-Lycaotinae (7-11), Heterarthrinae-Allantinae-Blennocampinae-Tenthredininae (7-12).
2. Straight ducts, uniformly broad: Nematinae (13), Susaninae (13), Diprionidae (13), Cimbicidae (13), Perginae (6).

Malpighian Tubules:

On embryological evidence (Johanssen and Butt, 35), a primitive insect is believed to possess six Malpighian tubules corresponding with the six embryological divisions of the rectum. Wigglesworth (68) describes the tubules as varying from three to eight in hymenopterous parasites and bees. The majority of literature references (68, 62) suggest uniformity in tubule number as well as

in arrangement. This is not the case in sawflies. As indicated in Tables 7, 8 and 9, tubule numbers vary from three to over 100, and tubule arrangements are of three types: (1), primitive, a low number entering the gut separately, extending freely anteriorly, others freely posteriorly or bound perirectally; (2), intermediate-advanced, many entering the gut separately, usually extending anteriorly some distance, and looping posteriorly; and, (3), advanced, one or more common stalks of branching tubules entering the gut.

Three factors are regarded as significant in establishing a "primitive" arrangement as a working hypothesis: (1) relatively low numbers of tubules; (2) individual attachment of the tubules to the gut; (3) anterior disposition of the tubules relative to the point of attachment. As proliferations of the mid-gut, the Malpighian tubules are assumed to pick up waste material in the body cavity (Wigglesworth, 68). In the many cases where they are bound to the rectum in a "crypto-nephridium" they are considered to have become functionally modified to reabsorb moisture from frass-pellets before extrusion. This condition, common in lepidopterous larvae, is a specialized or fairly advanced stage. In the Xyelidae (unanimously believed to be a primitive group) and in the Selandriinae (the primitive subfamily of the Tenthredinidae) the tubules have a primitive arrangement as defined above. The specialized Malpighian tubules, functionally ideal, should provide maximum penetration of the body cavity, have a firm junction with the rectum for moisture reabsorption, and have developed an efficient division of labour either within a single tubule or between tubules. Specialization has been attained through two types of modified arrangement: (1), an increase in number wherein each tubule extends anteriorly some distance to serve the anterior body cavity, then loops posteriorly to filter the posterior body cavity, and there, is bound perirectally; and (2), the tubules extend anteriorly, laterally, or posteriorly, the latter usually bound perirectally and all or most fuse in common collecting stalks before their entrance to the mid-gut. These two types are described as "intermediate-advanced" and "advanced" respectively and are regarded as alternate trends of specialization.

In keeping with the "primitiveness" of a low tubule number, Table 7 shows most species in the six to ten group, the range however being from three to 20. Where 18 to 20 tubules are found, they are always in a group showing a range upwards from a lower number, and the arrangement is primitive in type (see the Xyelidae). The spacing on the whole, is fairly even, the rectal binding is usually loose or absent. It is noteworthy that all the groups examined in the Orthandria (*sensu* Ross) except the Pamphiliidae, possess the primitive type of Malpighian tubule arrangement, with the Xiphydriidae and Cephidae characterized by a pattern which is a simple advance over that of the Xyelidae and Siricidae.

The level of advance reached in the Malpighian tubules of the Pamphiliidae is unusual in view of the fairly primitive position postulated for the family and its extreme similarity to the four families just mentioned. The similarity in primitive number and arrangement of the tubules of all species of the Selandriinae, Dolerinae, Athaliinae, and Lycaotinae examined, is one of the writer's reasons for suggesting that the four be reduced to tribal status in an enlarged Selandriinae. *Allantus calceatus* and *Dimorphopteryx pinguis* of the Allantinae belong in this primitive group on the basis of Malpighian tubules. If *A. calceatus* and *A. cinctus* are congeneric, as they are stated to be, an interesting and exceptionally wide intrageneric trend is evident, and it is possible to trace the origin of the genus in the Allantinae close to the separation point of the Allantinae-Blennocampinae from the other subfamilies in the Tenthredinidae. *Dimorphopteryx* appears to be a very primitive form either in the Allantinae, or in another group altogether.

TABLE VII. — Malpighian Tubules: Primitive Arrangement.

Species	T. No.	Spac.	Dispos. Type	R.B.	Type
Xyelidae:					
<i>Xyela minor</i>	5	E	b.2	C	1
<i>Pleroneura borealis</i>	10	E	b.2	C	1
<i>Macroxyela ferruginea</i>	20	C	b.10	C	1
Pergidae:					
Acordulecerinae:					
<i>Acordulecera</i> sp.....	10	E	b.6	B	1
<i>Acorduleceros</i>	8	E	a	B	1
Blasticotomidae:					
<i>Blasticotoma</i> (See Table 8).....	4				
Diprionidae:					
<i>Monoctenus</i> (See Table 8).....	10				
Tenthredinidae:					
Selandriinae:					
<i>Hemilaxonus dubitatus</i>	8	E	c.2	B	2
<i>Hemilaxonus</i> sp. 1.....	10	E	c.4	B	2
<i>Hemilaxonus</i> sp. 2.....	14	E	c.2	B	2
<i>Strongylogaster laticus</i>	10	E	c.2	B	2
<i>Strongylogaster macula</i>	9	E	b.1, c.2	B	2
<i>Selandria serva</i>	10	E	c.4	B	2
<i>Aneugmenus</i>	12	E	c.4	B	2
Dolerinae:					
<i>Dolerus vestigialis</i>	12	E	b.2, c.2	B	2
<i>Dolerus aericeps</i>	16	E	c.4	B	2
<i>Dolerus cothurnatus</i>	18	E	c.8	B	2
<i>Dolerus triplicatus</i>	20	E	c.4	B	2
Heterarthrinae:					
<i>Profenusa pygmaea</i>	4	E	a	B	5
Nematinae:					
Cladiini:					
<i>Priophorus</i> sp.....	15	E	a	C	2
Nematini:					
<i>Hoplocampa</i> (See Table 8).....	12				
<i>Caulocampus acericaulis</i>	6	E	c.2	B	2
<i>Anoplonyx</i> sp. (See Table 8).....	14				
Pseudodineurini:					
<i>Kerila</i> (See Table 8).....	9				
"Athaliinae":					
<i>Athalia rosae</i> , <i>Athalia</i> sp. 1.....	10	E	c.4	B	2
<i>Athalia himantopus</i> , <i>Athalia liberta</i>	10	E	c.4	B	2
<i>Athalia</i> sp. 2.....	9	E	a	B	5
Allantinae:					
Allantini:					
<i>Allantus calceatus</i>	8	C	b.2	B	1
Eriocampini:					
<i>Dimorphopteryx</i>	10	E	b.2. c.2	A	2
Blennocampinae:					
Lycaotini:					
<i>Lycaota</i>	12	E	b.2	B	2
Siricidae:					
Siricinae:					
<i>Sirex noctilio</i>	8	E	b.1	B	2(3)
<i>Sirex cyaneus</i>	6	C	b.2	B	2
Tremicinae:					
<i>Tremex</i>	6	E	b.2	B	1(3)
Xiphydriidae:					
2 <i>Xiphydria</i> spp.....	8	C	b.1	B	4
Cephidae:					
<i>Cephus cinctus</i> final instar, non-feeding.....	3		b.1	B	4

T. No. — Tubule Number

Spac. — Spacing of Tubules

E — equi-distant.

C — clumping tendency.

R.B. — Rectal Binding.

A — tubules float freely posteriorly.

B — loose posterior binding.

C — normal posterior binding.

D — double posterior binding.

Dispos. Type — Disposition of Tubules according to type.

a — all tubules posteriorly extending.

b — number of tubules posteriorly extending indicated viz. .1, .2 etc.

c — number of tubules extending from dorsal to ventral surface before turning posteriorly.

Type — According to Fig. 152.

TABLE VIII — Malpighian Tubules: Intermediate Arrangement

Species	T. No.	Spac.	Dispos. Type	R.B.	Type
Pamphiliidae:					
<i>Acantholyda</i> sp. 1.....	72	C	f.2-6	D	8
<i>Acantholyda</i> sp. 2.....	60	C	f.2-5	D	8
<i>Cephalcia</i>	48	C	f.2-9	D	8
<i>Pamphilus</i>	72	C	f.3-9	D	8
<i>Neurotoma</i>	36	C	f.5,W	D	8
Perginae:					
<i>Perga</i>	36	C	e	C	7
<i>Cereales</i>	18	C	e	C	7
Pterygophorinae:					
<i>Lophyrotoma</i>	42	E	d.2	C	6
Blasticotomidae:					
<i>Blasticotoma</i>	4	E	a	C	6
Pergidae:					
Diprionidae:					
<i>Monoclenus</i>	10	E	d.3	C	6
2 <i>Diprion</i> (<i>Gilpinia</i>) spp.....	24	E	c	C	6
Remaining Diprionidae.....	28	E	c	C	6
Tenthredinidae:					
Susaninae:					
<i>Susana</i>	40	E	c.1	C	6
Nematinae:					
Cladiini:					
<i>Cladius isomerus</i> , <i>Trichiocampus</i>	28	E	b	C	6
<i>Cladius pectinicornis</i>	22	C(ds)	b	C	6
<i>Priophorus rubivorus</i>	22	E	b	C	6
<i>Priophorus padi</i>	22	C	b	C	6
Nematini:					
<i>Hoplocampa</i>	12	C(vs)	d.1-3,	C	6
<i>Anoplonyx</i>	14	E	d.1	C	6
<i>Pikonema alaskensis</i>	28	E	b	C	6
<i>Croesus latipes</i>	28	G.1	d.1-2	C	6
<i>Amawronematus</i>	22	G.2	b	C	7
<i>Nematus</i> (<i>Pteronidea</i>) <i>leuchotrochus</i>	30	G.2	d.1	C	7
<i>Croesus septentrionalis</i>	34	E	d.1	C	6
<i>Platycampus</i>	21	G.1	c,d.1,	C	7
<i>Pristiphora winnipeg</i>	20	E	d.1	C	6
<i>N.</i> (<i>Pteronidea</i>) <i>ventralis</i> , <i>N.</i> (<i>P.</i>) <i>ribesii</i>	28	G.1	d.1-3,	C	7
<i>N.</i> (<i>P.</i>) <i>pavida</i>	22	C	d.1	C	6
<i>N.</i> (<i>Pontania</i>).....	8	E	d.1	C	6
<i>N.</i> (<i>P.</i>) <i>melanaspis</i>	28	C(ds)	d.2	C	6
<i>N.</i> (<i>P.</i>) <i>olfaciens</i>	28	C(vs)	d.1	C	6
<i>N.</i> (<i>Holcocneme</i>).....	38	E	b	C	6
<i>Pristiphora geniculata</i>	28	C(ds)	d.1	C	6
Remaining Nematini.....	28	E	d.1	C	6
Psuedodineurini:					
<i>Kerita</i>	9	E	c,d.1	C	6

T. No. — Tubule Number

Spac. — Spacing of Tubules

E — equi-distant

C — clumping

C(vs) mid-ventral space

C(ds) mid-dorsal space

G — group or band formation

.1 band, regular, distance anteriorly, irregular

.2 posteriorly extending band

Dispos. Type — Disposition of Tubules According to Type

a — $\frac{2}{3}$ gut length anterior loopb — $\frac{1}{5}$ c — $\frac{1}{8}$ c.1 less than $\frac{1}{8}$ d.1 — $\frac{1}{12}$ d.2 — more than $\frac{1}{12}$ d.3 — less than $\frac{1}{12}$

e — directly anteriorly and posteriorly extending

f. — tubule range per clump

f.W. — wing-like modification

R.B. — Rectal Binding

A — tubules float freely posteriorly

B — loose posterior binding

C — normal posterior binding

D — double posterior binding

Type — According to Fig. 152

TABLE IX
Malpighian Tubules: Advanced Arrangement

Species	Dispos. Type	Tubule No.	R.B.	Type
Argidae:				
Arginae:				
<i>Arge pectoralis</i> , <i>A. clavicornis</i> , 3 <i>Arge</i> spp.....	I.1a	38	C	9
<i>Arge annulipes</i>	I.2aw	24	C	9
<i>Arge ochropus</i>	I.2bs	16	C	9
<i>Arge sugilloides</i>	I.2c.1	16	C	9
<i>Arge</i> sp. 1.....	I.2b	16	C	9
<i>Arge micheli</i>	I.2c.2	16	C	9
Atomacerinae:				
<i>Atomacera</i>	III.a	10	C	9
Sterictiphorinae:				
<i>Sterictiphora</i>	III.a	16	C	9
Sericocerinae:				
<i>Sphacophilus cellularis</i>	III.b	14	C	9
<i>Sphacophilus plumiger</i>	III.c	14	C	9
<i>Sofus</i>	I.1a	10	C	9
<i>Schizocera</i>	I.2c	18	C	9
Cimbicidae:				
<i>Zaraea</i> , <i>Abia</i>	III.d.1	14	C	9-10v
<i>Trichiosoma</i>	IV.d.2	10	C	9-10v
<i>Cimbex americana</i>	V.d.1	100	C	10
<i>Cimbex</i>	III.d.1	100	C	10v
Tenthredinidae:				
Heterarthrinae:				
Caliroini:				
<i>Endelomyia aethiops</i>	III.e.1	8	B	12
<i>Caliroa fasciata</i>	III.e.2w	24	B	12
<i>Caliroa cerasi</i>	III.e.3w	16	B	12
Heterarthrini:				
<i>Heterarthrus</i>	III.e.1	7	B	11v
Fenusini:				
<i>Parna</i>	III.c.2	6	B	12
<i>Metallus pumilus</i>	II.d.2	7	B	11v
<i>Metallus geii</i>	II.d.2.v.	18	B	13-14
<i>Fenusa ulmi</i>	IV.d.2	7	B	11
<i>Fenusa dohrnii</i>	III.d.2	7	B	11
<i>Fenusa pusilla</i>	III.e.1	7	B	11v
Allantinae:				
Allantini:				
<i>Empria</i> (<i>Parataxonius</i>).....	VI.d.1	20	B	9v
<i>Ametastegia</i> (<i>Protemphytus</i>) <i>pallipes</i>	IV.d.2	8	B	14
<i>Ametastegia</i> on <i>Spiraea</i>	IV.e.1	8	B	13-14
<i>Monostegia</i>	II.d.2	8	B	14
<i>A. (P.) carpini</i>	II.d.2.Hf	8	B	13v
<i>A. (P.) equiseti</i>	II.d.2.Sf	8	B	13v
<i>A. (P.) perla</i>	III.d.2	8	B	13
<i>Macremphytus</i> sp. 1.....	I.f	10	B	9v
<i>Allantus cinctus</i>	IV.d.2	16	B	15v
<i>Apthymus</i>	IV.d.2	8	B	14
<i>Macremphytus</i> sp. 2,3.....	II.d.2z	8	B	14v
<i>Macremphytus</i> sp. 4.....	IV.d.2	6	B	14v
Eriocampini:				
<i>Eriocampa ovata</i>	III.e.4	16	B	12v
<i>Pseudosiobla</i>	II.d.2	12	B	
Blennocampinae:				
<i>Tomostethus multicinctus</i>	IV.d.2Sl	14	B	15
<i>Tomostethus nigrilus</i>	IV.d.1Sl	22	B	15
<i>Pareophora minuta</i>	IV.e.1	10	B	15
<i>Rhadnoceraea</i>	II.d.2	12	B	12
<i>Phymatocera</i>	II.e.5w	20	B	13
<i>Perichista albida</i>	II.d.1Sf	15	B	13
<i>Perichista</i> sp.....	IV.e.1	12	B	15
<i>Blennocampa pusilla</i>	II.d.2Pf	9	B	12
<i>Monophadnoides geniculatus</i>	II.d.1Rf	9	B	12

TABLE IX
Malpighian Tubules: Advanced Arrangement—*Continued*

Species	Dispos. Type	Tubule No.	R.B.	Type
<i>Tenthredinidae:—Continued</i>				
<i>Tenthredininae:</i>				
<i>Lagium</i>	IV.d.2	26	B	15v
<i>Aglaostigma</i>	V.d.2	16	B	15v
<i>Tenthredopsis</i> sp. 1.....	IV.d.1	24	B	15
<i>Tenthredopsis litterata</i>	IV.d.2	16	B	15
<i>Tenthredo scrophulariae</i>	V.d.1	18	B	15
<i>Tenthredopsis nassata</i>	II.d.1C	18	B	16
<i>Tenthredopsis</i> sp. 2.....	II.d.1C	24	B	16
<i>Tenthredo obsoleta</i>	II.d.1	26	B	12
<i>Tenthredo colon</i>	II.d.1S	16	B	12
<i>Tenthredo zona</i>	III.d.2z	12	B	12
<i>Macrophya epinola</i>	II.d.1v.2	24	B	12
<i>Tenthredo</i> sp.....	II.d.1v.1	22	B	12
<i>Cephidae:</i>				
<i>Cephus cinctus</i> feeding stage larva.....	III.d.2	10	B	12

DISPOS. TYPE—Disposition of tubules, according to type

Dispos.—

- I — 2 stalks, general posterior direction
 .1 well-separated
 .2 almost fused
 II — 2-stalk structure still apparent,
 anteriorly directed
 III — 1-stalk, anteriorly directed
 IV — 2 stalks, anteriorly directed
 V — more than 2 stalks, separate entrances
 VI — 2 stalks, laterally directed
 90° with mid-ventral line.

- Sf — strap-like fusion
 Hf — half-fusion, rounded
 Pf — rounded fusion
 Rf — rectangular fusion
 C — crescentic
 SI — strap-like
 .3w, wing branching posterior tubules
 .4w, wing-branching parallel to mid-ventral line
 .5w, wing-branching anteriorly, posteriorly, laterally
 f — posterior stalks modified, some anterior tubules

Type—

- a — 45°, posteriorly directed branches,
 w—wing-like expansions
 s—sac-like entrance
 b — 60°, posteriorly directed branch
 tubules
 c — 90°, with mid-ventral line
 .1 branching far out
 .2 branching close
 d — 45° anteriorly directed branches
 .1 anterior, posterior and lateral
 branches
 .2 anterior, posterior tubules only
 v — V-shaped fusion
 .1-wide
 .2-tight
 z — loose attachment
 e — branches parallel to mid-ventral line
 .1 anterior and posterior straight
 .2w wing branching parallel to
 mid-and hind junction, anterior
 and posterior tubules.

R.B. — Rectal Binding
 See Table 8

TYPE — According to Fig. 152
 v — variation from type

Profenusa pygmaea, characterized by a low number and by V-shaped fusion, is considered a relatively specialized "primitive" representative of Heterarthrinae. *Priophorus* sp. and *Caulocampus acericaulis* are presumably primitive members of the intermediate-advanced Cladiini and Nematini respectively.

The intermediate-advanced Diprionidae and Cladiini are characterized by strikingly homogeneity in tubule numbers, arrangement, and general disposition (Table 8). So uniform is the pattern formed in each, by the looping anteriorly of each tubule that except for the occurrence of the occasional numerical variation or difference in spacing it is impossible to separate the component species on the basis of Malpighian tubules. In the Nematini, despite variable numbers, irregular

dispositions, and frequent clumping tendencies, the majority of species possess an identical tubule pattern and are largely inseparable on this basis. In the Perginae, the absence of looping and the degree of fusion in the mid-ventral tubules in the two species examined, suggest a specialized condition within the intermediate-advanced group. In Pamphiliidae, a further modification is found in the clumping of tubules of general intermediate-advanced pattern, and their extension directly posteriorly to a double perirectal binding.

In the advanced group (Table 9), the rather homogeneous Malpighian pattern of the Argidae reveals a general trend from the widely-separated, posteriorly-directed stalks of the Sericocerinae, via the *Arge pectoralis* group, to *A. micheli* and *A. ochropus* of the Arginae to the anteriorly-directed common branch stalks of the Atomacerinae. In the Cimbicidae, the *Zaraea-Abia* arrangement is close to the general level attained by *Atomacera* in the Argidae; the species of *Cimbex* seem the least advanced, and those of *Trichiosoma* intermediate. Judging from the anterior direction of both the main common branch and the branch stalks, the *Zaraea-Abia* pattern resembles even more closely that of the Heterarthrinae-Allantinae-Blennocampinae-Tenthredininae than that of the Argidae.

In all tribes of the Heterarthrinae, the general arrangements are the same as, or approaching in form, the 3 by 1 type (Fig. 152, 12 and 13) and the same type is found throughout the Allantinae, Blennocampinae, and Tenthredininae. Definite trends are apparent in the tubules of the Allantinae, as follows:

Empriini:

1. Generalized, 2-stalk arrangement:
 - a. Lateral stalks, posteriorly extending tubules, few anterior.....*Empria* (*Parataxonus*)
 - b. Angled stalks, 3 by 1 arrangement.....*Ametastegia* (*Ametastegia*) *pallipes*
 - c. Right-angled stalks, parallel to mid-venter.....*Ametastegia* sp. on *Spiraea*
2. Fusion:
 - a. Two-stalk origin still apparent.....*Monostegia abdominalis*
 - b. Strap-like.....*A. (A.) carpini, equiseti*
3. Simple yet specialized single stalk condition.....*A. (A.) perla*

Allantini:

1. Tubules entering separately.....*Allantus calceatus*
2. Two-stalk formation directed posteriorly.....*Macremphytus* sp. 1
3. Two-stalk formation directed anteriorly:
 - a. Angled stalks, more tubules than 3 by 1 arrangement.....*Allantus cinctus*
 - b. 3 by 1 arrangement.....*Apethymus braccatus*
 - c. Modification of 3 by 1 to 2 by 1 arrangement.....*Macremphytus* sp. 4
4. Fusion, 2-stalk origin still apparent.....*Macremphytus* sp. 2, 3

Eriocampa and *Pseudosiobla* of the Eriocampini show a complete fusion of stalks, the former having extensive anterior projections.

A similar survey of the tubules in the Blennocampinae reveals the following trends:

1. Two-stalk condition (most generalized within subfamily):
 - a. Lateral sweep.....*Tomostethus nigratus*, *T. multicinctus*, *Periclista* sp.
 - b. With reduction in tubules.....*Pareophora*

2. Fusion:

- a. Two-stalk origin still apparent.....*Rhadinoceraea*
 b. Straight line*Phymatocera*
 this species a link to the crescentic arrangement so prominent in the
Tenthredininae.
 c. Strap-like-Single tubule reduction, mid-ventral anterior tubule present
Periclista albida, Monophadnoides

3. Single stalk (most advanced condition within subfamily).....*Blennocampa*

There is no indication of a primitive arrangement in any one of the species examined. The tubule arrangement of *Tenthredopsis nassata* is typical of the *Tenthredininae*, but there is considerable variation within the subfamily (as shown below) and some species are very similar to typical representatives of the *Allantinae* and *Blennocampinae*.

1. Generalized 2-stalk formation:

- a. Separate entrances*Aglaostigma*
 b. Right-angled stalks*Tenthredopsis* sp.

2. Fusion, origin of 2-stalks still apparent.....

Tentredo obsoleta, Tentredo colon

3. Single stalk.....*Tentredo zona, Tentredo* sp., *Macrophya epinota*

TABLE X
 Malpighian Tubule Summary

Group	Primitive	Intermediate	Advanced
Xyelidae.....	+	-	-
Blasticotomidae.....		+	-
Pamphiliidae.....	-	+	-
Xiphydriidae.....	+Sp.	-	-
Cephidae.....	+Sp.	-	+
Siricidae.....	+Sp.	-	-
Pergidae:			
Acordulecerinae:.....	+	-	-
Pterygophorinae:.....	-	+	-
Perginae:.....	-	+	-
Argidae.....	-	-	+
Cimbicidae.....	-	-	+
Diprionidae.....	(1)	+	-
Susaninae.....	-	+	-
Tenthredinidae:			
Selandriinae:.....	+	-	-
Group 1 Dolerinae:.....	+	-	-
Athaliinae:.....	+	-	-
Lycaotinae:.....	+	-	-
Nematinae:			
Cladiini:.....	(1)	+	-
Group 2 Nematini:.....	(1)	+	-
Pseudodineurini:.....		+	-
Heterarthrinae:.....	(1)	-	+
Allantinae:			
Allantini:.....	(1)	-	+
Group 3 Eriocampini:.....	(1)	-	+
Blennocampinae:.....	-	-	+
Tenthredininae:.....	-	-	+

+ indicates type present

- indicates type absent

Sp. — specialized

(1) no. of species of given type

TABLE XI — Miscellaneous Characters

Species	Gastric Caeca	Divert- icula	Crypts	Glands
Xyelidae:				
<i>Macroxyela</i>				Ia
Pamphiliidae:				
<i>Neurotoma</i>			Gmr	
<i>Cephalcia, Acantholyda</i> sp. 1, 2			Gmr	
Pergidae:				
Acordulecerinae:				
<i>Acordulecera</i>			Gs	IIa
Perginae:				
<i>Perga</i>	M	P		
<i>Cerealces</i>	B	P		
Pterygophorinae:				
<i>Lophyrotoma</i>	Rs			
Argidae:				
Arginae:				
<i>Arge pectoralis</i>	R	Gt		IIb
<i>Arge annulipes</i>	R			IIb.1
<i>Arge micheli</i>	R			
<i>Arge ochropus, A. sugilloides</i>	R	Gt		
<i>Arge</i> sp. 1				IIb
Atomacerinae:				
<i>Atomacera</i>	R			IIc
Sterictiphorinae:				
<i>Sterictiphora</i> sp.	R			IIc
Sericocerinae:				
<i>Sphacophilus cellularis</i>		Gs		IIe
<i>Sphacophilus plumiger</i>	R	Gt		IIe
<i>Sofus</i>		Gr		IIe
<i>Schizocerus</i>	R			IIe
Cimbicidae:				
<i>Zaraea</i>		Gt	Os	IIc
<i>Abia</i>		Gt	Gs	IIc
<i>Cimbex americana</i>		G	Gs	IIc
<i>Cimbex, Trichosoma</i>			Gs	IIc
Diprionidae:				
<i>Monocerus</i>		O		
<i>Neodiprion</i> spp. <i>Diprion</i> (<i>Diprion</i>), <i>Diprion</i> (<i>Gilpinia</i>)		O	Gmr	
Nematinae:				
<i>Cladlini</i>				Ib
<i>Nematini</i> (Except <i>Pikonema alaskensis</i>)				Ib
Allantinae:				
Eriocampini:				
<i>Eriocampa</i>		Grc		
Tenthredininae:				
<i>Aglaostigma</i>		Grc		
Siricidae:				
Tremicinae:				
<i>Tremex</i>		Gr		

GASTRIC CAECA

- M — Maltese-cross shaped
 B — button-like
 R — rectangular-lobulate
 Rs — rectangular-squared lobulate

CRYPTS

- O — oesophageal
 G — gastric
 s — single cell
 m — multi-cellular
 mr — multi-cellular in rings

DIVERTICULA

- O — oesophageal
 G — gastric
 s — simple
 t — typhlosole-like
 r — ring-formation
 rc — complete ring
 P — pharyngeal

GLAND TYPES

- I — eversible
 a — cervical
 b — ventral abdominal
 II — non-eversible
 a — external, sucker-like
 b — ventral abdominal
 .1, single pair
 c — spiracular
 d — milk-bottle glands
 e — pontoon glands
 f — conically projecting

As in the Blennocampinae, there is no indication of a primitive Malpighian tubule arrangement in the Tenthredininae.

It is questionable whether more than coincidence is involved in the "primitive", "intermediate-advanced", and "advanced" groupings that so clearly segregate species of the Diprionidae, the Argidae, and the Cimbicidae for example, and the three subfamily "groups" in the Tenthredinidae (see Table 10). That a greater range of variability might be revealed by examination of more species in all groups is remote, considering the wide range of distribution of species studied.

Although the Malpighian tubules are useful for segregation of species, and for establishing trends of specialization within genera and families, the occurrence of parallel evolutionary trends in different families limits their usefulness in broad phylogenetic studies. For example, in the Argidae and Cimbicidae which are quite distinct in regard to broad salivary gland characters, parallel evolution is indicated by the degree of similarity in Malpighian tubule development.

Miscellaneous Structures:

Additional characters, which may prove to be of phylogenetic significance, may be divided into four classes (see Table 11).

(1) Those definitely characteristic of entire groups and hence presumably of some phylogenetic consequence, e.g., oesophageal diverticula of the Diprionidae, pharyngeal diverticula of the Perginae; gastric caeca of the Arginae, Atomacerinae, Sericocerinae, Sterictiphorinae, Pterygophorinae, and the Perginae; and the ventral abdominal eversible glands of the Nematinae (except for *Pikonema alaskensis*).

(2) Those apparently restricted to groups but which require more comprehensive study before their determinative value is evident, e.g., the cervical glands in some species of Xyelidae; the ventral abdominal non-eversible glands of some Argidae; the distribution of the fat body; and the presence of rectal teeth in conifer and sedge feeders.

(3) Those of interest in species identification, e.g., differences in cuticular covering; presence or absence of spines, setae, and cuticular glands; and structure of slime glands, wax glands, and glandubae.

(4) Those showing gradation in closely related groups although their value as phylogenetic indices is doubtful, e.g., presence or absence of crypt-like protuberances on the gut (Cimbicidae, Acordulecerinae) and of crypt-like regions (Diprionidae); variations in gut proportions, including the size and structure of crop; variations in the epithelial lining of the gut; and the structure of the individual Malpighian tubules.

PHYLOGENY

Perhaps one of the most striking features in Yuasa's work is his tendency to follow, even with misgivings, the classification of MacGillivray, who based his generalizations on sawfly wing venation. Yuasa's Tenthredinidae, therefore embraced 24 subfamilies, including the Hylotominae (now the Argidae), Diprioninae, and Cimbicinae. Other workers have felt that according these last-mentioned groups family status would off-set any tendency towards making the Tenthredinidae inclusive of a greater range of variability than other families, e.g. Pamphiliidae or Xyelidae. Internal anatomical detail, however, demonstrates a trend in the salivary glands from the Argidae through the Acordulecerinae and Pterygophorinae (of the Pergidae); to the primitive, intermediate, and advanced Tenthredinidae; to the Perginae, Diprionidae, and Cimbicidae. One of Benson's reasons for including 14 somewhat linked groups as subfamilies in a Pergidae complex was to conform to the concepts of accepted family limits. Should the trends and similarities within the 14 subfamilies of the Pergidae (*sensu* Benson) be such that only subfamily status should be accorded them, then the Yuasa-MacGillivray theory of a Tenthredinidae complex of 24 families should be re-appraised, since the Argidae, Diprionidae, and Cimbicidae are integral parts of character-trends apparent throughout the Tenthredinoidea (*sensu* Ross) and subtend no greater variation as families than do the members of the Pergidae complex as subfamilies. On the other hand, should homogeneity of form be considered a fundamental criterion for the application of the term "family" to a group, it would be reasonable to break up Benson's pergid subfamily complex by elevating its components to family status, and to subdivide the Tenthredinidae into its postulated "three groupings" (see Table 10), recognizing the apparent trends by relative disposition of families instead of by subordinating groups to subfamily status. Internal as well as external larval anatomy favours emphasis being placed on a large number of suitably linked families or subfamilies within the Tenthredinoidea.

Internal anatomy establishes three sawfly groupings: (1) the Xyelidae, (2) the old Orthandria minus the Xyelidae, and (3) the Tenthredinoidea, including the Blasticotomidae. The salivary glands accentuate the intermediate position of the Xyelidae close to the main ancestral sawfly stem that gave rise to the types found among the Tenthredinoidea, on the one hand, and the remaining old Orthandria, on the other. In general this study confirms Yuasa's theory that the Xyelidae are on the direct line from which the Tenthredinoidea (Strophandria) descended, since although the xyelid salivary gland structure permits the derivation of both the incorporated salivary type (Orthandria) and the free type (Strophandria), it is closer to the latter. On a species level, internal anatomy is overwhelmingly in agreement with Ross' arrangement based on adult characters, e.g. the trends within the Tenthredininae, Allantinae, and Blennocampinae; however, although trends are established in other groups, e.g. the Cimbicidae, they do not necessarily confirm sequences by Ross based on adult characters. Striking confirmation is provided for Benson's fusion of the Selandriinae and Dolerinae, and his formation of a large Blennocampinae complex.

Admittedly internal anatomical detail alone is scarcely sufficient foundation on which to base sweeping generalizations as to phylogenetic trends or taxonomic arrangements. The facts, however, provide not only strong corroboration for general trends as outlined by Benson and Ross, but also evidence for a more detailed arrangement as shown in Fig. 153.

The ancestral sawfly larva, the writer believed, possessed fairly compact salivary glands, with anterior reservoirs, slender collecting ducts surrounded by large tightly packed individually attached salivary-gland cells. The Malpighian tubules, between the embryological six and ten in number, entered the gut separately, some anteriorly, some posteriorly-extending, mostly free-floating in the body cavity. Following the first line of development indicated in Fig. 153, the xyelid salivary arrangement represents an intermediate stage between the looser free gland-cell type of Line 2 and the fully incorporated gland-cell type of Line 3. The Malpighian tubules are also primitive in arrangement. Larval Megalodontidae were not available but are included, on the basis of external larval and adult descriptions, with the Pamphiliidae. The Pamphiliidae show the first tendency towards incorporation of the gland cells into the duct lining, with some cells remaining free and individually attached to the duct. The tubules, all posteriorly coiling, are a modification of the advanced-intermediate type with a high degree of fusion into clumps.

Following Line 3, the salivary glands of the wood-boring Xiphydriidae and Siricidae show complete incorporation of gland cells into the duct lining, along the entire length of the duct with the retention of reservoirs in the former; and with a telescoping of the incorporated gland-cell region into short compact sacs, an absence of reservoirs, and a squaring of ducts, in the latter. The Siricidae are characterized by a simple primitive arrangement of few tubules, whereas the Xiphydriidae, retaining a low tubule number, show a degree of V- and Y-shaped fusion. A doubling of the number of salivary glands occurs in the Cephidae, the glands themselves resembling those of the Xiphydriidae. The Malpighian arrangement, Y-shaped fusion in type, appears an advance over that of the Xiphydriidae. Both wood- and stem-borers show a streamlining of body form and tendency towards relative decrease in mid-gut length.

The purely strophandrious line of development (2) is broadly divided, after the branching of the Blasticotomidae, into two parts as suggested by Ross (52), a pergid group and a cimbicid-tenthredinid-diprionid group. The tenthredinid section is enlarged to include three "natural" subfamily groupings (identified at C, D, and E), each of which subtends no greater variation than do the Cimbicidae and Diprionidae. Along Line 2, there is a general loosening of the free yet compact coating of salivary-gland cells about a slender duct. Point A marks the branching of the Blasticotomidae with salivary-gland cells free, yet forming a loosely compact sheath about the ducts, slender reservoirs, and a low Malpighian number and primitive arrangement. Upon internal anatomical evidence, the Blasticotomidae could equally well have been derived from Line 1.

At Point B, the main pergid groups branch off. Some members of the Argidae retain one set of salivaries reminiscent of the Xyelidae and Blasticotomidae, or an accompanying set of slender ducts and numerous minute side branches connecting grape-like clusters of salivary-gland cells. Pronounced gastric caeca are characteristic of almost all Argidae. All Argidae show a tendency to ventral abdominal non-eversible glands. An advanced Malpighian tubule arrangement, consisting of two stalks of posteriorly extending tubules, varying in specific details of arrangement, is typical of the Argidae. A slightly modified salivary arrangement in the Acordulecerinae, absence of gastric caeca, retention of low tubule number and arrangement, places them close to the B junction. The position of the Pterygophorinae is also close to Junction B. The salivary arrangement is somewhat argid-like, with slender, main branch ducts, lined by single rows of gland cells; gastric caeca are present, and the Malpighian tubules are advanced-intermediate in type. The position of the Perginae is

postulated as close to or at the B junction. In the Perginae the salivary ducts are expansible into wide ducts of even diameter, clusters of gland cells joining the broad ducts by fairly long side-branches. This arrangement appears intermediate between the argid salivary type and the broad salivaries to be found in the remaining groups. Gastric caeca and pharyngeal diverticula are present and the Malpighian tubules are advanced modifications of the intermediate-advanced type.

A change to expansible salivary ducts has occurred near Junction B and there is an accompanying change to smaller salivary-gland cells. The final junction, labelled CDE, groups the expanded Tenthredinidae (including Cimbicidae and Diprionidae). Point D marks a continuation of the primitive arrangement in Malpighian tubules in the Selandriinae, Athaliini, Lycaotini, and the Dolerinae. The Strongylogasterini of the Selandriinae possess salivary ducts with alternate bulb-like expansions and narrow junctions, with reservoirs and flattened cuboidal cells. The Selandriini lack reservoirs and possess shorter junctions. The Dolerinae possess two sets of salivary glands and lack reservoirs. The Athaliini have a squared, alternately expanded salivary arrangement, with or without reservoirs, and the Lycaotini show a trace of alternation of ducts and a suggestion of reservoirs. The Malpighian tubule similarity of all four groups, in conjunction with the general salivary similarity, is the basis of this primitive subfamily grouping within the Tenthredinidae.

Three main subgroups are included in the E branching, the Nematinae with three compact tribes (*Pikonema alaskensis* is an exception because of the absence of ventral abdominal eversible glands), the Susaninae, and the Diprionidae. All groups lack reservoirs. The Cladiini are characterized by a doubling or trebling of salivary-gland number and variation in duct type, with narrow ducts present as well as ducts with alternate expansions. There is a trace of alternate expansion and junctions in the more primitive of the Nematini and uniformly wide ducts in the Pseudodineurini. Malpighian tubule arrangement is typically intermediate-advanced in all three tribes. The Susaninae and Diprionidae have oesophageal diverticula, uniformly wide expansible salivary ducts, and intermediate-advanced Malpighian tubules. On the other hand, a possible origin of the Diprionidae from the main stem before the CDE junction, is more in keeping with its present family status. Although this position links its Malpighian arrangement with that found in the Perginae and Pterygophorinae, the writer favours the first interpretation, namely grouping the Diprionidae, Susaninae, and Nematinae as intermediate-advanced forms in the enlarged Tenthredinidae.

Line C tends to segregate four tenthredinid subfamilies and the Cimbicidae in an advanced grouping. In the Heterarthrinae, there are salivary reservoirs in the Caliroini only, and a telescoping of the alternations in the ducts; the faintest trace of alternation of salivary ducts is found in the Fenusini, and none in the Heterarthrini. There is an indication of alternation in some Blennocampinae and Allantinae, none in the Tenthredininae. The Malpighian tubule pattern of the four subfamilies is strikingly similar although it is possible to describe a "typical" allantine (*Monostegia*), blennocampine, (*Periclista*), tenthredinine (*Tenthredopsis*) and heterarthrine (*Heterarthrus*). One member of the Cimbicidae possesses a reservoir. Cimbicid salivary ducts are uniform in diameter and the Malpighian tubules repeat the general arrangement found in the four subfamilies of the Tenthredinidae, especially the Tenthredinine pattern with the overlapping of tubules. An alternate origin of the Cimbicidae is shown before the CDE junction. The writer, however, favours its inclusion in the group of advanced Tenthredinidae. *Allantus calceatus* and *Dimorphopteryx pinguis* are

illustrated as exceptions because the Malpighian tubules are primitive in number and general arrangement.

From the larval ancestor postulated by Yuasa as having larvapods on abdominal segments 1-10, subanal appendages on segment 11, and multi-segmented antennae, Line 1 follows a tendency towards loss of larvapods and subanal appendages, to the Xyelidae, Megalodontidae, and Pamphiliidae. There is a loss of larvapods and subanals in the Xyelinae, subanals in the remaining Xyelidae, and of larvapods in the Megalodontids and Pamphiliids. The thoracic legs of the last two families are seta-like as opposed to the normal legs of the Xyelidae.

There is a complete loss of larvapods along Line 3; a modification of thoracic legs ranging from fleshy, mamma-like to vestigial structures; a tendency towards loss of subanals, complete in the first branching, incomplete in the cephid branch; modification of antennae and of annulation, and appearance of a suranal process which is lost again in the extremely modified Orussidae.

Line 2 shows a tendency towards loss of subanal appendages and extreme variability in larvapod number. The Blasticotomidae are characterized by a complete loss of larvapods, retention of subanal appendages, 5-segmented antennae, and three annulets in the third abdominal segment. Four annulets, a complete loss of larvapods, and "waffle-like" single-segmented antennae are found in the Perginae. Three annulets, larvapods on 2-8 and 10, "waffle-like" antennae, and an anal tail characterize the Pterygophorinae. Three annulets, traces of larvapods on 2-7 and 10, 6- to 7-segmented antennae, thoracic-leg empodia, sucker-like glands on the latus and apparently 6-segmented thoracic legs are found in the Acordulecerinae. The Argidae possess three annulets, variable numbers of larvapods on segments 2-6, 2-7, 2-8, 2-9, and on all ten abdominal segments as well as on 4-8 and 10; flat-mosaic to low conical antennae of 2-3 segments, thoracic legs apparently 6-segmented with empodia, and variable types of external glands. Beyond Junction B larvapods are present on abdominal segments 2-7 and 10 or 2-8 and 10, and there are never more than five segments to the larval antennae, with the larvae in the CDE grouping showing remarkable homogeneity in form. Group D is characterized by larvapods on 2-8 and 10, seven annulets in the Selandriinae (6 in the remaining members) and 5-segmented antennae. Group E possesses larvapods on 2-7 and 10 in the Nematinae, 2-8 and 10 in the Diprionidae and Susaninae. The Nematinae have 4 to 6 annulets, 4- to 5-segmented antennae either flat or low mound, and ventral abdominal eversible glands (except *Pikonema alaskensis*). Six annulets are found in the Susaninae and Diprionidae with 5-segmented spike antennae in the former, 4- to 5-segmented flat antennae in the latter. In the advanced Group C, larvapods are present on segments 2-8 and 10 with 7 annulets in the Tenthredininae and the Cimbicidae, 6 in the Allantinae, 5 to 6 for the Blennocampinae, 6 in the Heterarthrinae except in the most highly modified forms. The Tenthredininae, Allantinae, and Blennocampinae possess 5-segmented spike antennae; 3- to 5-segmented, usually spiked antennae are found in the Heterarthrinae, and the antennae of the Cimbicidae are button-like and reduced.

The adult sawfly progenitor postulated by Ross possessed a simple head capsule, distinct sternopleural sutures, slender multi-segmented antennae, and tibiae with two unmodified apical and at least one to four preapical spurs. Along Line 1 there is a tendency towards turned or strophandrious male genitalia as seen in the Xyelinae; a tendency towards a trapezoidal mesosternum in the Megalodontidae and towards a closed head capsule. Basal or intermediate hamuli are present and the 2nd radial cross-vein is joined to Rs proximad of the 2nd radio-

medial cross-vein. A large presternal bridge is present. The third antennal segment is elongate in the Xyelidae but not in the other two families.

Line 3 shows retention of orthandrious male genitalia and a triangular mesosternum; the large presternal bridge is absent, basal or intermediate hamuli are present and the 2nd radial cross-vein joins Rs proximad of the 2nd radio-medial cross-vein. In the Siricoidea there is a genapontal head, an absence of preapical tibial spurs, and a tendency towards extreme consolidation of thorax and abdomen. The component families possess fused or partly-fused paraglossae and alaglossae, a secondary transverse suture across the mesoscutum, a tentorium reflected antero-ventrally, a complete ventral migration of the antennae in the Siricidae, and of the clypeus and part of the frons, as well, in the extremely modified Orussidae. In the Cephidae, there is a maxapontal head, retention of preapical spurs, venation somewhat as in the Siricoidea, close union of meta- and mesonotum and the first abdominal tergite, and a marked constriction between the first and second abdominal terga.

Line 2 shows entirely strophandrious male genitalia, a trapezoidal mesosternum, open head-capsule; absence of basal or intermediate hamuli; 2nd radial cross-vein, if present, joins Rs distad of 2nd radio-medial; simple male genitalia without parapenes, and loss of sterno-pleural sutures and preapical spurs in all but the most primitive species in each group. The Blasticotomidae possess a xyelid-like elongation of a third antennal segment and a minute fourth segment; the radial cell is crossed by a vein; the abdomen laterally carinate. This general description of characters for Line 2 holds throughout the pergid-argid group. Benson gives a characteristic which holds for the Perginae, Pterygophorinae, and Acordulecerinae; this is the retention of the cell Rs and the disappearance of M. Antennae along the pergid-argid branch show a tendency toward reduction. In the Pterygophorinae, they are multi-segmented and flagellate; in the Acordulecerinae they are 6-segmented; in the Perginae they are reduced clavate and in the Argidae, 3-segmented with a single thick flagellum. Beyond the B branching the male genitalia have parapenes, there is a complete loss of sterno-pleural sutures and preapical spurs with the three families developing their own peculiar characteristics, capitate antennae in the Cimbicidae, laterally carinate abdomen (see Blasticotomidae); 13 or more antennal segments in the Diprionidae, serrate in the females, pectinate in the males; setaceous (sometimes clavate) antennae with 7-10 segments in the Tenthredinidae, and the presence of a post-tergite.

The writer is aware that the chief criticism of the preceding arrangement would be that the similarities leading to the groupings might be in the level of evolution. As stressed previously, it is believed that the wide representation of species within the various taxonomic groups and the absence of exceptions of grouping characters among these species serve to weaken, if not nullify, this criticism. The arrangement emphasizes the general trends to be found throughout the sawflies which must be explained before a "natural" order may be established and illustrates the existing lack of balance in the levels assigned to the various groups.

Both Benson and Ross stress that a complete correlation of all larval and adult information available is necessary, and that there is a demand for the application of as many morphological characters as possible. The writer is convinced that, in sawflies, internal larval anatomy provides an additional tool not extensively used to date.

Calman (15) has stated, "it often happens that closer study will enable us to define species limits even in cases where they are not obvious in first inspection

and it is the constant hope of the systematist when dealing with a difficult group that he may light upon some character previously unrecognized that will give him the necessary clue". In this case the chosen characters submitted are internal anatomical; they clearly provide clues to evolutionary trends as valid as those derived from adult and external larval morphology.

SUMMARY

A study of 132 recognized species of sawflies has demonstrated the value of internal anatomical detail as a taxonomic tool and as an additional indicator of possible phylogenetic relationships. Two characters are of major importance, the salivary glands and the Malpighian tubules.

1. The accepted cleavage of the sawflies into two primary groups, with the Tenthredinoidea on the one hand, the Megalodontoidea, Siricoidea, and Cephoidea on the other, is corroborated by the larval salivary-gland character and added confirmation is provided for Benson having accorded superfamily status to the Xyelidae, and for Yuasa's theory that they stand close to the point of initial dichotomy of the two main sawfly divisions. A similarly intermediate position is evidenced for the Blasticotomidae.
2. Intra-family variability ranges, in such groups as the Diprionidae, Argidae, Cimbicidae, Xyelidae, and Pamphiliidae, are revealed that establish family limits more firmly in these primitive Hymenoptera.
 - A. The Perginae are shown to have affinities with the Diprionidae and the Cimbicidae, and the Acordulecerinae and Pterygophorinae with the Argidae. This, combined with a gradual character trend throughout the Tenthredinoidea from the Argidae to the Diprionidae and Cimbicidae, calls for a readjustment of family and subfamily limits to subtend approximately the same degree of variability.
 - B. In supporting Benson's concept of the extremely close relationship of the Selandriinae and Dolerinae, and of the subfamilies in his extended Blennocampinae, the writer would add the Athaliinae and, possibly the Lycotini to the first group, the Heterarthrini and Tenthredininae to the second. Evidence is set forth that the division of the Tenthredinidae into three main subfamilies permits assessment of relationships and comparative positions. Malpighian tubule evidence discloses three evolutionary levels with similar trends traced within the various levels.
3. Trends within genera frequently confirm Ross and Benson, particularly in *Arge*, *Dolerus*, *Tenthredopsis*, and *Ametastegia*. New species fitted into the general internal anatomical scheme are considered phylogenetically.
4. Recognized aberrant forms and anomalies in classification proved such in internal anatomical characters as well. Advocated removal of species from allotted positions is sometimes validated by discrepancies in internal anatomy (viz; *Pikonema alaskensis*); elsewhere the primitive or specialized nature of the species is emphasized as responsible for taxonomic difficulties.
5. Finally, internal anatomy allows identification of unrecognized Old World larvae that otherwise can be keyed only to a certain level in New World classifications, of undescribed larvae found associated, or believed associated, with known or suspected adults, and of larvae in unworked groups where the details establish relationships to other known groups.

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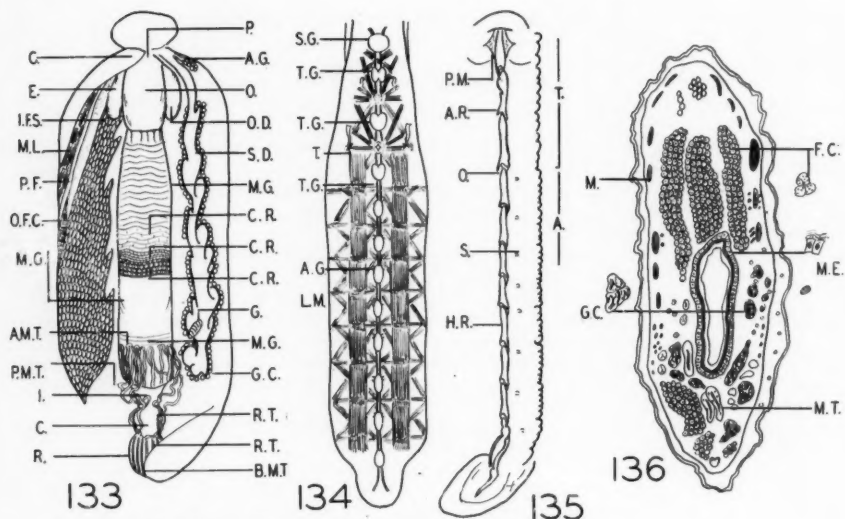
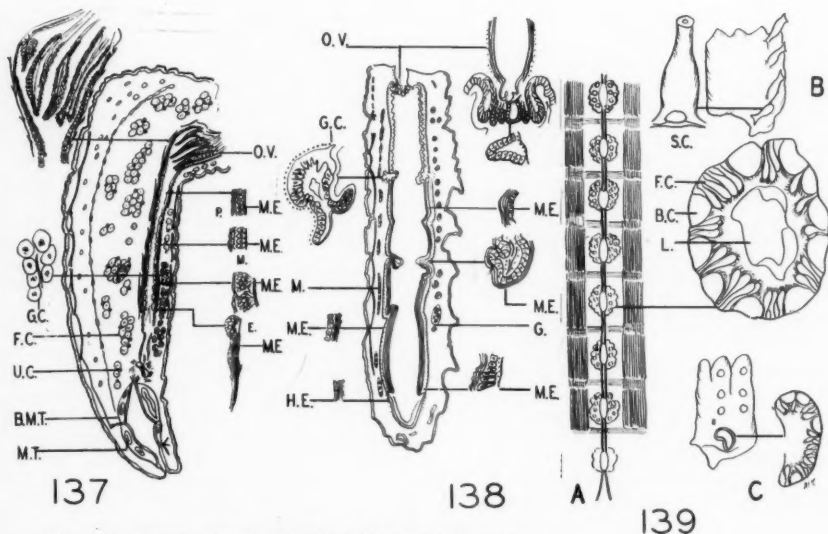
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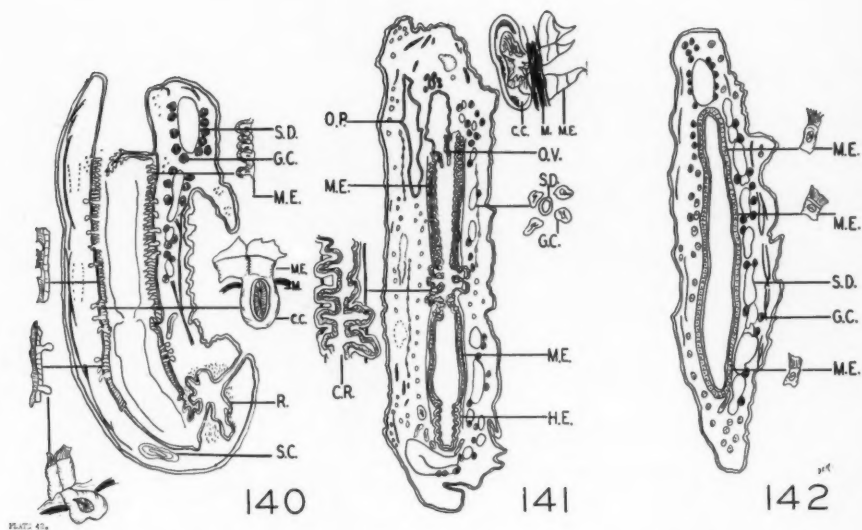
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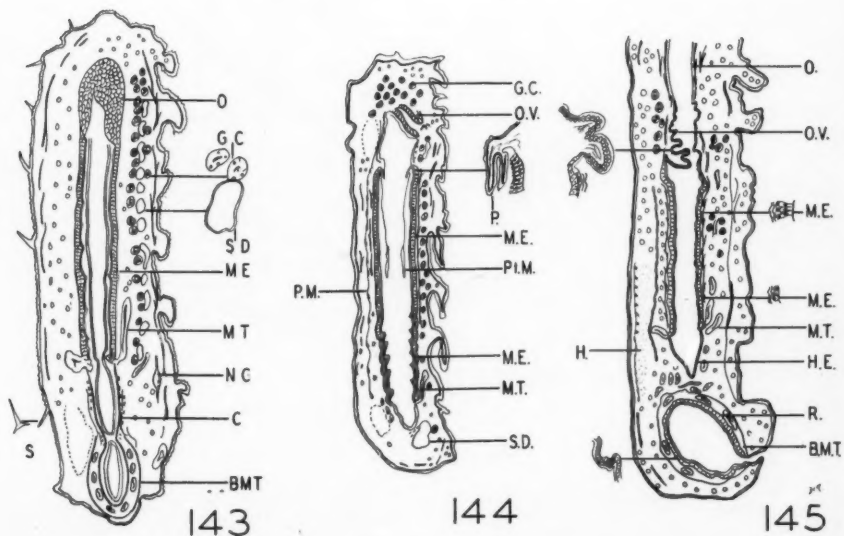
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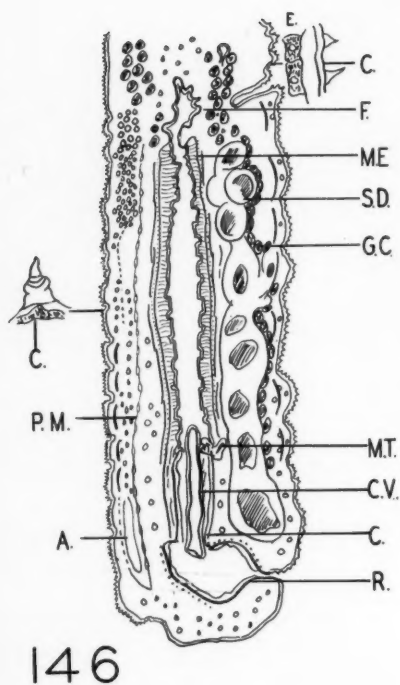
Fig. 133. *Neodiprion lecontei*—Gross larval dissection.Fig. 134. *Neodiprion lecontei*—Nerve cord and ventral muscle distribution.Fig. 135. *Neodiprion lecontei*—Heart and aorta.Fig. 136. *Pteroneura borealis*—Longitudinal histological section.Fig. 137. *Pamphilius*—Longitudinal histological section.Fig. 138. *Arge pectoralis*—Longitudinal histological section.Fig. 139. A. Location of ventral abdominal non-eversible glands in *Arge pectoralis* in venter dissection with camera lucida tracing of one gland in histological section.B. Lateral view of body segment with location of "milk-bottle" glands of *Atomacera*, camera lucida enlargement of a single gland.C. Lateral view of abdominal segment with location of a "sucker" gland in *Acordulecera* sp. with camera lucida tracing of one gland in section.



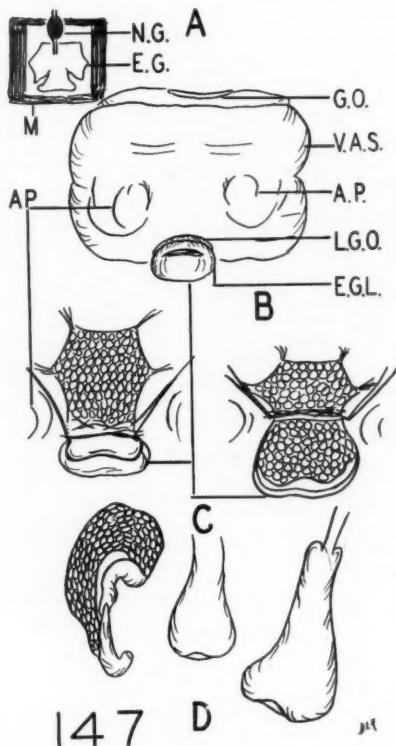
Figs. 140. *Cimbex americana*. 141. *Diprion (Gilpinia) bercyniae*. 142. *Femusa ulmi*.



Figs. 143. *Cladius isomerus*. 144. *Pristiphora erichsonii*. 145. *Pikonema alaskensis*.



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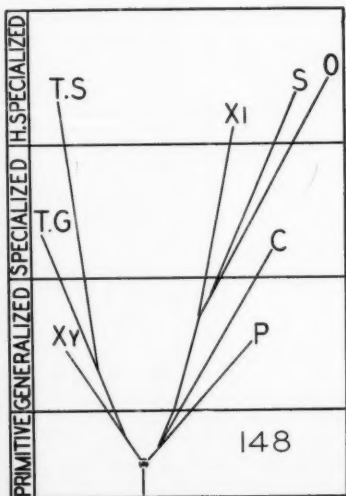
Fig. 146. *Tomostethus multicinctus*.

Fig. 147. A. Location of a ventral abdominal eversible gland in dissection of the venter in *Nematus* sp.

B. Location of a ventral abdominal eversible gland externally.

C. Views of gland in everted and non-everted positions.

D. View of a fully everted typical gland.

Fig. 148. Chart of the classification of sawfly larvae taken from Yuasa (69).

T.S.—specialized Tenthredinidae.

T.G.—generalized Tenthredinidae.

Xy.—Xyelidae, Xi.—Xiphydriidae, O.—Orussidae, S.—Siricidae, C.—Cephalidae, P.—Pamphiliidae.

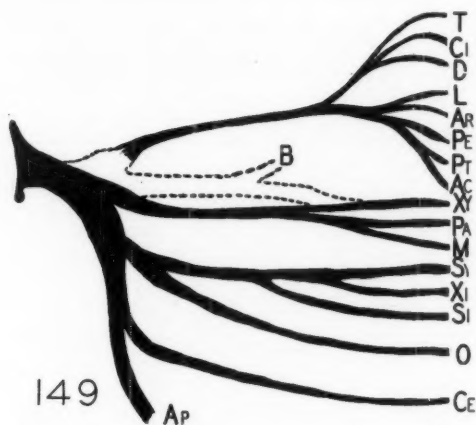


Fig. 149. Chart of the classification of sawfly adults (superfamilies and families) taken from Ross (52). Dotted lines indicate a modification added by the writer on the basis of internal larval study. T.—Tenthredinidae, Ci.—Cimbicidae, D.—Diprionidae, L.—Loboceridae, Ar.—Argidae, Pe.—Pergidae, Pt.—Pterygophoridae, Ac.—Acorduleceridae, B.—Blasticotomidae, Xy.—Xyelidae, Pa.—Pamphiliidae, M.—Megalodontidae, Sy.—Syntectidae, Xi.—Xiphydriidae, Si.—Siricidae, O.—Oryssidae, Ce.—Cephidae, Ap.—Apocrita.

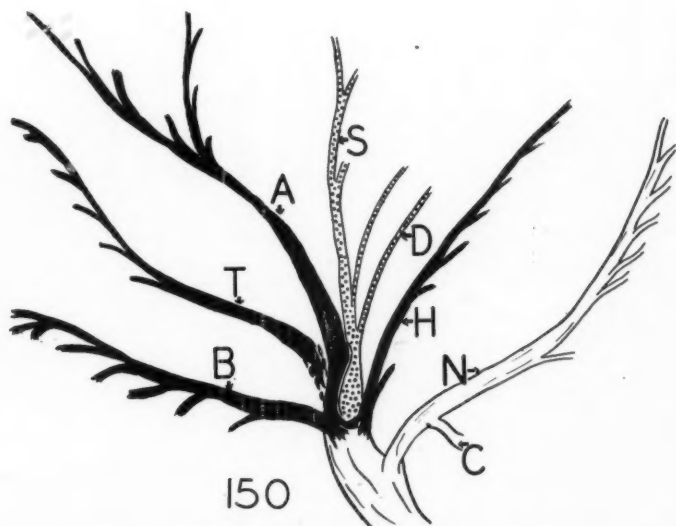


Fig. 150. Chart of the classification of sawfly adults in the subfamilies of the Tenthredinidae, taken from Ross (52). The shading indicates three possible groupings on the basis of the internal anatomy according to the writer: Group 1. PRIMITIVE: the dotted lines, S.—Selandriinae, D.—Dolerinae (Plus the Athaliinae and the Lycaotinae not shown); Group 2. INTERMEDIATE-ADVANCED, the white, N.—Nematini and C.—Cladiini (subfamilies in 1937, plus the Pseudodineurini); and Group 3. ADVANCED, the black, A.—Allantinae, T.—Tenthredininae, B.—Blennocampinae, and H.—Heterarthrinae.

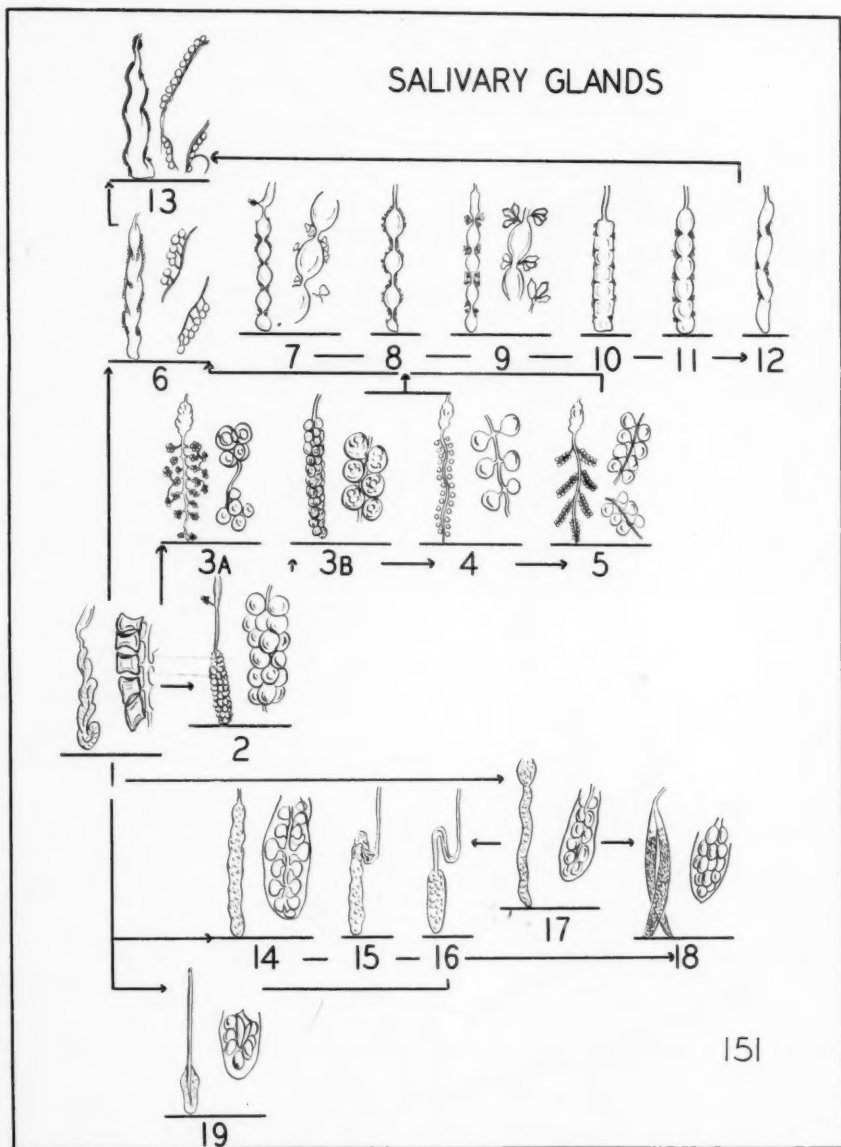
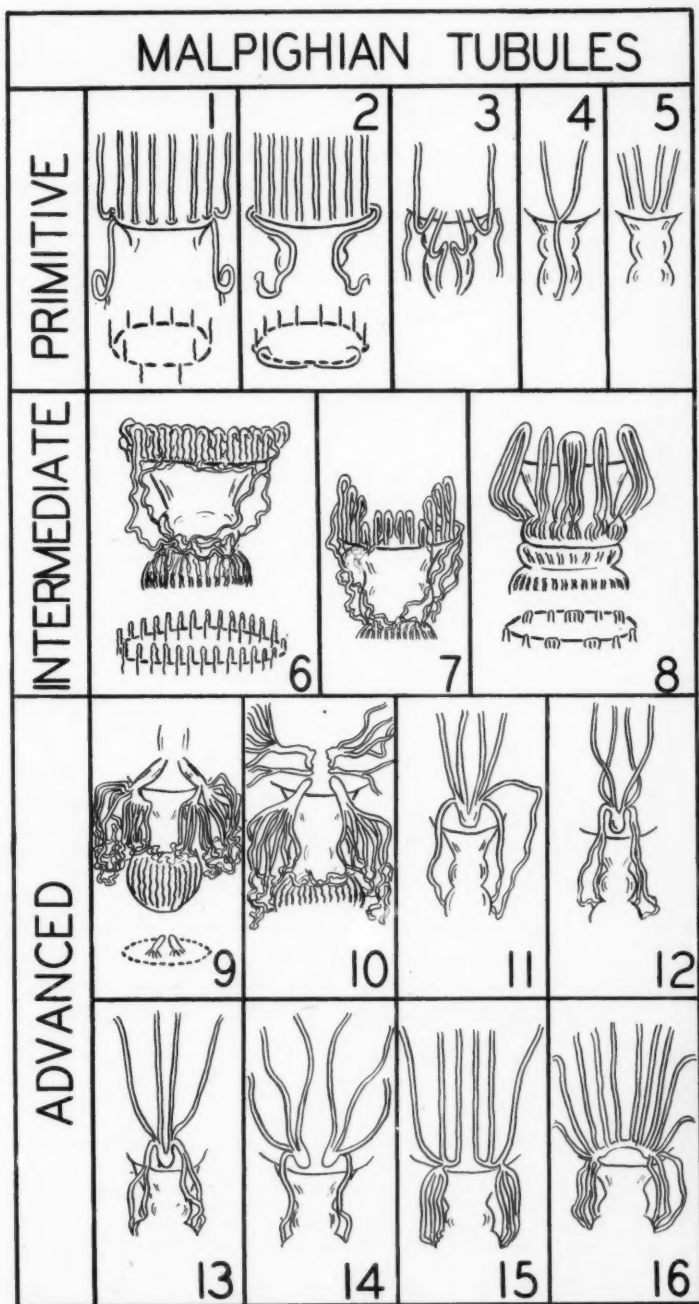


Fig. 151. General Phylogenetic chart of sawflies on the basis of the larval salivary glands. 1.—Xyelidae, 2.—Blasticotomidae, 3.—A & B—two gland types of some Argidae, 4. Pergidae (Atomacerinae), 5.—Pergidae (Pterygophorinae), 6.—Pergidae (Perginae), 7-12.—variations in the alternate enlargement and narrow-junction type of salivary found in the Selandriinae, Dolerinae, Athaliinae, Heterarthrinae, Allantinae, Blennocampinae, and some Tenthredininae possibly. 7.—typical gland with reservoir and flattened cuboidal cells, 8.—modification—elongate junctions, 9.—elongate, pear-shaped cells as in Athaliini, 10.—squared, bulb-like expansions, 11.—telescoped bulbs, 12.—only trace of alternation in gland, 13.—Diprionidae, Cimbicidae, some Tenthredinidae, 14-15-16.—Pamphiliidae, 17.—Xiphydriidae, 18.—Cephidae, 19.—Siricidae.

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Fig. 152. Summary chart of Malpighian tubules of the postulated PRIMITIVE, INTERMEDIATE-ADVANCED, and ADVANCED types of arrangement.

1.—Xyelid-type.
 2.—Selandriid variation of 1.
 3.—Siricid variation of 1.
 4.—Cephid variation.
 5.—Xiphydriid variation.
 6.—general Nematine, Cladiine-Diprionid type.
 7.—Nematine and Pergid variation.
 8.—Pamphiliid variation.
 9.—Argid-type.
 10.—Cimbicid variation.
 11.—advanced type with unequal branching as characterizing some Heterarthrinae.
 12.—general advanced type.
 13.—predominant pattern in Heterarthrinae.
 14.—in the Allantinae.
 15.—in the Blenno-campinae.
 16.—in the Tenthredininae illustrate the extreme similarity in these groups.



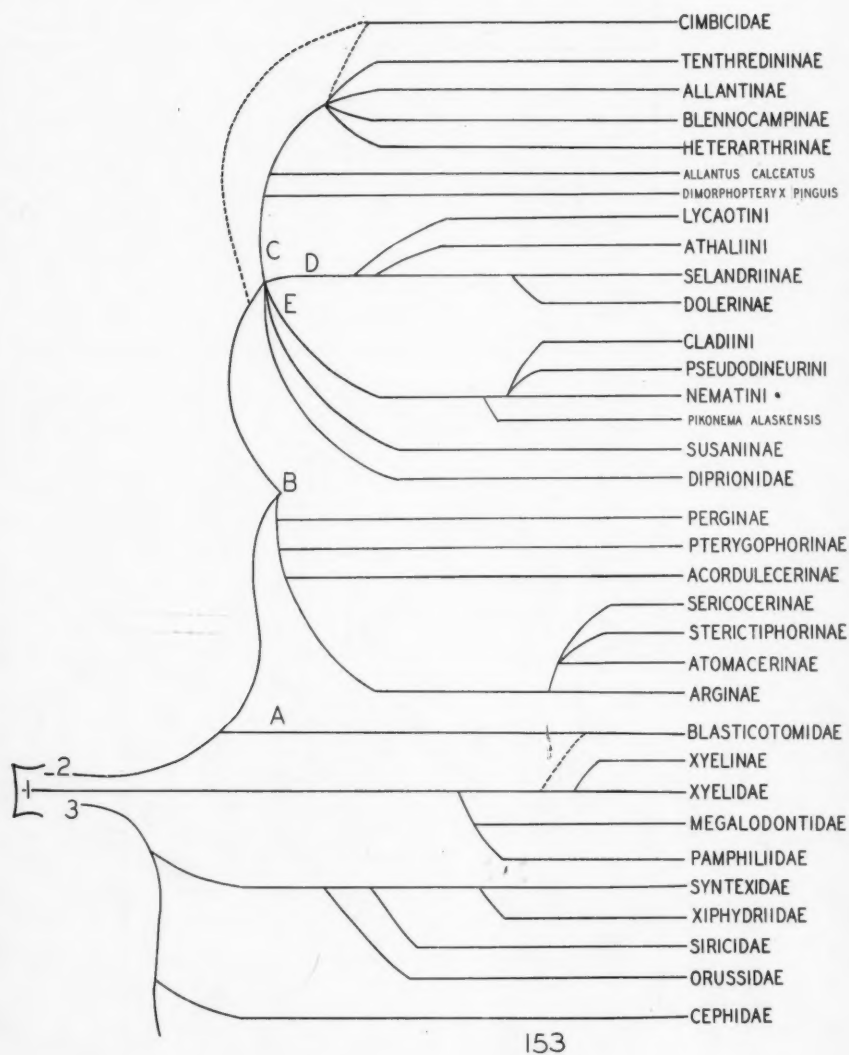


Fig. 153. Postulated phylogenetic arrangement of sawflies on the basis of internal larval anatomy, as well as correlated external larval and adult morphological data. Characters arranged in Table 12. 1. Xyelid primitive line, 3. Line accompanying parasitic, wood-boring habits, possibly to the Apocrita, 2. Line of Tenthredinoidea, A. Blasticotomid branch-off, B. Argid branching (Perginae complex although Perginae and Pterygophorinae may leave farther along Tenthredinoidea stem), C. Advanced grouping of the Tenthredinidae, D. Primitive, E. Intermediate-Advanced.

